OCCASIONAL PAPERS

of the
MUSEUM OF NATURAL HISTORY
The University of Kansas
Lawrence, Kansas

SYSTEMATICS OF THE LEPTODACTYLID FROG GENUS
TELMATOBIUS IN THE ANDES OF NORTHERN PERU

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ABSTRACT   The taxonomic status of populations of *Telmatobius* (Anura: Leptodactylidae) in the Peruvian departments of Amazonas, Cajamarca, La Libertad, and Piura is evaluated using an evolutionary species concept and data from external morphology, osteology, morphometrics, larval morphology, and allozyme electrophoresis. Nine species are recognized, and a key for identification is presented. The three named species are redescribed using the type specimens and newly collected material. These species are: *T. brevipes* Vellard, from the Cordillera Occidental of Cajamarca and La Libertad; *T. ignavus* Barbour and Noble, from the Cordillera Huancabamba in Piura; and *T. latirostris* Vellard, from the city of Cutervo in Cajamarca. Lectotypes are designated for *T. brevipes* and *T. latirostris*. Six species are described as new. *Telmatobius atahualpai* inhabits high elevations in the Cordillera Central in Amazonas. *Telmatobius colanensis* is known from a single specimen from the Cordillera Colán in Amazonas. *Telmatobius degener* and *T. thompsoni* are sympatric species from a locality in the Cordillera Occidental of La Libertad. *Telmatobius degener* is characterized by several unusual osteological features, and is the only known anuran that lacks premaxillary teeth but retains maxillary teeth. *Telmatobius necopinus* is known from the lower slopes of the Cordillera Central. *Telmatobius truebae*, found at several localities in the Cordillera Central, is externally similar to *T. necopinus*, but is distinct osteologically and biochemically, and is not the sister taxon of that species. Striking variability in the morphology of the columella (middle ear bone) is described within and among species. Generic assignment of the nine species is argued phylogenetically, and the genus *Telmalsodes* is placed in the synonymy of *Alsodes*.

Key words: Leptodactylidae; *Telmatobius; T. atahualpai, T. colanensis, T. degener, T. necopinus, T. thompsoni, T. truebae;* New species; Peru; Systematics.

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RESUMEN   Se estudió la sistemática del género leptodactílido de ranas *Telmatobius* en los Andes del norte del Perú. Se analizó el status taxonómico de poblaciones de *Telmatobius* en los departamentos de Amazonas, Cajamarca, La Libertad, y Piura aplicando un concepto evolutivo de especie y usando datos de morfología externa, osteología, morfometría, morfología de renacuajos, y aloenzimas. Los análisis revelaron la existencia de nueve especies en esta zona. Se justifica filogenéticamente la asignación de estas especies al género *Telmatobius*. Las tres especies descritas fueron redescrita usando el material tipo y material nuevo. Estas especies son: *T. brevipes* Vellard, de la Cordillera Occidental de Cajamarca y La Libertad; *T. ignavus* Barbour and Noble, de la Cordillera de Huancabamba en Piura; y *T. latirostris* Vellard, se conoce solamente de la ciudad de Cutervo en Cajamarca. Se designan lectotipos de *T. brevipes* y *T. latirostris*. Se describen seis especies como nuevas. *Telmatobius atahualpai* es un habitante de las partes altas de la Cordillera Central en el Departamento Amazonas. *Telmatobius colanensis* se conoce solo un espécimen de la Cordillera de Colán en Amazonas. *Telmatobius degener* y *T. thompsoni* son especies simpátricas de una localidad en la Cordillera Occidental en La Libertad. *Telmatobius degener* se caracteriza por muchos rasgos osteológicos. *Telmatobius necopinus* se conoce de una ladera baja de la Cordillera Central en Amazonas. *Telmatobius truebae*, se encuentra en varias localidades en la Cordillera Central en Amazonas, es externamente similar a *T. necopinus*, pero es distinta en caracteres osteológicos y bioquímicos, y no es el taxón hermano de esta especie. Se describe la notable variación en la morfología de la columela (hueso medio del oido) dentro y entre las nueve especies. Se presenta tambien una clave de identificación y datos sobre la ecología.

Palabras claves: Leptodactilidos; *Telmatobius; T. atahualpai, T. colanensis, T. degener, T. necopinus, T. thompsoni, T. truebae;* Especies nuevas; Peru; Sistematica.

The leptodactylid frogs of the genus *Telmatobius* are a diverse and problematic group from the central and southern Andes mountains of South America. Thirty species and 30 subspecies of *Telmatobius* were listed by Frost (1985). Since then, one species has been transferred to another genus (*Phrynopus juninensis*, Cannatella, 1985) and five new species have been described (*T. scrocchii*, Laurent and Lavilla, 1986; *T. hypselocephalus* and *T. platycephalus*, Lavilla and Laurent, 1988a; *T. pinguiculus* Lavilla and Laurent, 1988b; *T. carrillae*, Morales, 1989). The genus ranges from southern Ecuador, through Peru and Bolivia, to the Andes of northern Argentina and Chile. Although *Telmatobius* are found between 1300 and 5000 m elevation (*T. ceiorum* and *T. marmoratus*, respectively), most species occur near 3000–3500 m (Cei, 1986). In general, *Telmatobius* are nocturnal, secretive, aquatic to semiaquatic frogs of moderate to large size.

As discussed by Trueb (1979) and Cei (1986), the systematics of *Telmatobius* is complex and difficult. Descriptions and diagnoses of most species are inadequate and not comparable among accounts. The existence of numerous subspecies suggests that the number of (evolutionary) species in the genus has been greatly underestimated. Cei (1986) and Trueb (1979)

discussed confusing and discordant patterns of inter- and intrapopulation variation in *Telmatobius*, and Trueb (1979) suggested that morphological data alone might be insufficient to resolve the status of some populations. Furthermore, supraspecific groupings based on explicit hypotheses of phylogenetic relationships have not been proposed, numerous species have been shown to have been incorrectly assigned to the genus (e.g., Lynch, 1978; Cannatella, 1985), and the monophyly of the genus remains highly suspect (e.g., Cei, 1986; Morales, 1989). Trueb (1979) began the onerous task of revising the genus with her revision of the *Telmatobius* of Ecuador.

In this paper I review the systematics of the genus in the adjacent geographic region, the Andes of northern Peru. More specifically, the purposes of this paper are to: (1) evaluate the status of *Telmatobius* populations from the departments of Amazonas, Cajamarca, La Libertad, and Piura using an evolutionary species concept and data from a diversity of character systems (external morphology, osteology, larval morphology, morphometrics, allozyme electrophoresis); (2) redescribe the three previously named species from the region (*T. brevipes* Vellard, *T. ignavus* Barbour and Noble, *T. latirostris* Vellard); (3) describe six new species; and (4) justify inclusion of these species in *Telmatobius*.

STUDY AREA

The physiography of northern Peru is dominated by the Cordillera Occidental, the Cordillera Central, and the Huancabamba Depression. The Huancabamba Depression is a system of low arid valleys (ca. 1000–2000 m above sea level) and isolated mountain ranges (including the Cordillera Colán and Cordillera Huancabamba) that separate the northern and central Andes (Duellman, 1979). South of the Huancabamba Depression, the central Andes are divided into the Cordillera Occidental and Cordillera Central by the low, arid valley of the Río Marañón. The lower Pacific slopes of the Cordillera Occidental are relatively arid, with desert at low elevations successively giving way to spiny forest, dry forest, cloud forest, and páramo (montane grassland above treeline), at the highest elevations (Tosi, 1960). The Cordillera Central is more lush, with páramo at the highest elevations, cloud forest at lower elevations, and subtropical rainforest on the lowest Amazonian slopes (Tosi, 1960). The geographic distribution of each species is shown in Figure 1, and their altitudinal distributions are shown in Figure 2.

MATERIALS AND METHODS

Decisions about the taxonomic status of populations should appeal to an explicit definition of what species are believed to be (e.g., Cracraft, 1992). In this study, I use an evolutionary species concept, as proposed by Simpson
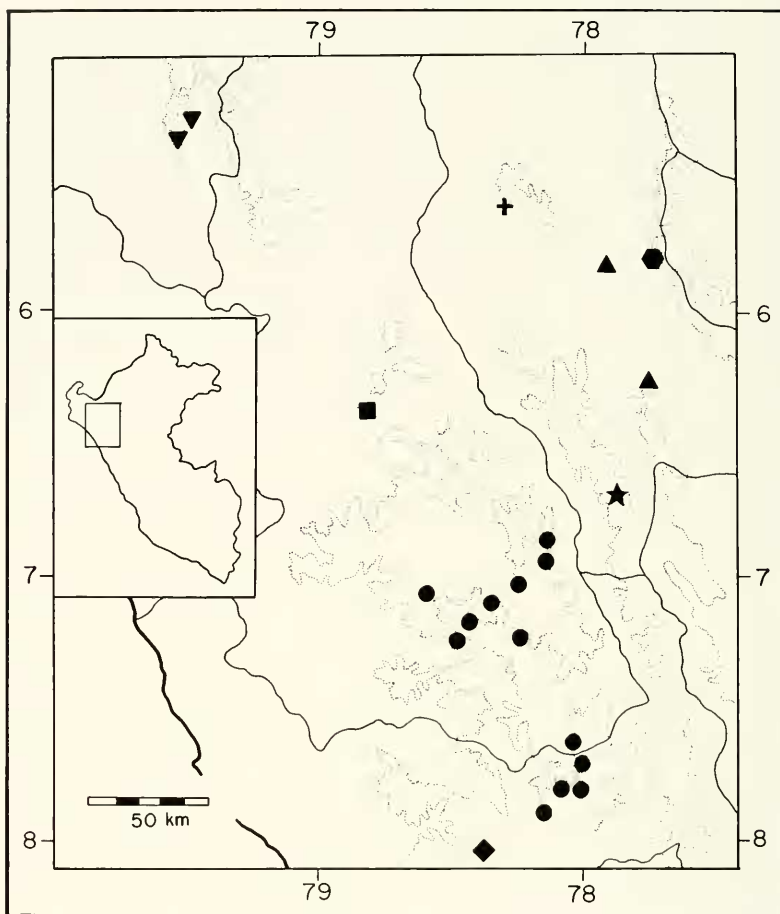
Fig. 1. Distribution of species of *Telmatobius* in northern Peru. *T. brevipes* (circles), *T. colanensis* (plus sign), *T. ignavus* (inverted triangles), *T. latirostris* (square), *T. necopinus* (hexagon), *T. truebae* (triangles), sympatric *T. degener* and *T. thompsoni* (diamond), and sympatric *T. atahualpai* and *T. truebae* (star). Localities are approximated from distances by road; multiple localities in close proximity are represented by a single symbol. Dotted lines show areas over 3000 m, solid lines indicate limits of Peruvian departments. The inset shows the location of the study area within Peru.

(1961) and modified by Wiley (1978) and Frost and Hillis (1990). Thus, I consider a biparental species to be the largest single lineage within which there is reproductive cohesion and which maintains its identity apart from other lineages through time. I favor this concept because it requires that the recognized taxa be logically consistent with evolutionary history (in con-
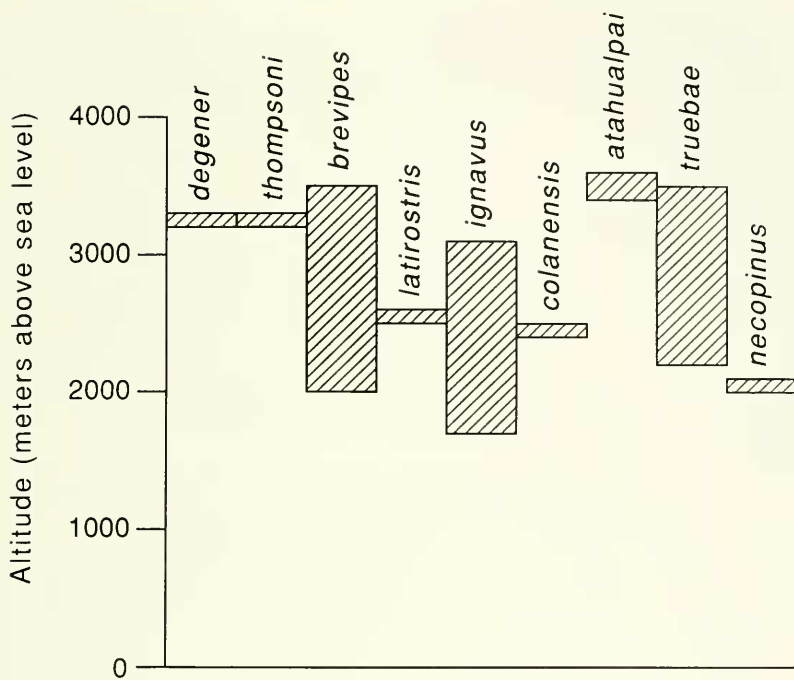
Fig. 2.   Altitudinal distributions of species of *Telmatobius* in northern Peru.

trast to the biological species concept) and avoids the philosophical pitfalls and potential overreductionism of the phylogenetic species concept (Frost and Hillis, 1990). The evolutionary species concept provides a general conceptual framework for recognition of species, rather than a set of strict operational rules (Frost and Hillis, 1990). In this study, I considered the following to be evolutionary species: (1) populations that apparently were isolated geographically (especially if they were morphologically and/or biochemically distinct); (2) diagnosable sympatric forms; and (3) groups of homogeneous, geographically contiguous populations that were presumed to be interbreeding and/or whose status as a single monophyletic lineage was not rejected by phylogenetic analysis of the allozyme data. Because delineation of real evolutionary entities can be a difficult and even subjective undertaking (e.g., Frost and Hillis, 1990), I consider it necessary to give a more explicit justification and explanation for species-level decisions than a mere listing of the distinguishing characters of the putative species. Taxonomic decisions made in this study are explained and discussed near the end of the Results section.

Over the course of the study, 221 preserved adult and subadult frogs (including the type material and newly collected specimens of the 3 de-

scribed species), 14 lots of tadpoles, 19 cleared-and-stained and dry skeletal preparations, and tissues from 21 individuals from northern Peru were examined (Appendix I). Institutional abbreviations are as follow: Museum of Natural History, The University of Kansas (KU), Louisiana State University Museum of Natural Science (LSUMZ), Museum of Comparative Zoology, Harvard University (MCZ), Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima (MHNSM, formerly MHNJP), Florida State Museum, University of Florida (UF). Terminology for external features generally follows Duellman (1970), and formulae for toe webbing follow Savage and Heyer (1967) as modified by Myers and Duellman (1982). Cleared-and-stained skeletons were prepared using a modified version of the technique of Dingerkus and Uhler (1977). Terminology for osteological features follows Trueb (1973) and Duellman and Trueb (1986).

For descriptive purposes and morphometric analysis, 12 measurements were recorded from adult specimens to the nearest 0.1 mm with needle-tipped calipers. These are abbreviated throughout as follows: SVL (snout-vent length), TIBL (tibia length; knee to heel), FOOT (foot length; proximal edge inner metatarsal tubercle to tip of fourth toe), HLEN (head length; posterior corner of jaw to tip of snout), HWID (head width; from posterior corner of jaw), IOD (interorbital distance), IND (internarial distance), ENOS (eye-nostril distance; from anterior corner of eye), EYE (eye diameter; between anterior and posterior corners of eye), HNDL (hand length; proximal edge of outer palmar tubercle to tip of third finger), THBL (thumb length; proximal edge inner palmar tubercle to tip of thumb), RDL (radioulnar length; elbow to distal edge of outer palmar tubercle). Sexual maturity was determined by presence of eggs in females (or relative size in large females without eggs) and development of the nuptial excresence in males. Descriptive statistics for these measurements were computed using the SYSTAT statistical package. Multivariate analyses of the morphometric data were performed using the SAS statistical package on the IBM mainframe computer system at the University of Texas at Austin. Multivariate techniques are described in the section on morphometrics. In the species descriptions, ranges of proportions are followed in parentheses by the mean, one standard deviation, and the sample size.

Tadpoles were staged according to the table of Gosner (1960). Terminology for larval characters follows Altig and Johnston (1989), and the format for tadpole descriptions follows McDiarmid and Altig (1990).

Allozyme electrophoresis provides invaluable data for inferring gene flow, phylogenetic relationships among closely related taxa, and species boundaries (Hillis and Moritz, 1990). These data are particularly useful in groups with complex patterns of inter- and intrapopulation morphological variation, such as *Telmatobius*. (See Cei, 1986, and Trueb, 1979, for

examples.) Tissues for electrophoretic analysis were obtained from nine populations of *Telmatobius* (representing 4 putative species) during the spring of 1989. Throughout the paper, the populations of *T. brevipes* sampled electrophoretically are numbered as follow: 1 = Cajamarca: 21 km NNW Cajamarca; 2 = Cajamarca: 8 km S Cajamarca; 3 = Cajamarca: 9 km S Celendín; 4 = La Libertad: 19 km SSE Cajabamba. Populations of *T. truebae* are labelled as follows: 1 = Amazonas: 11 km SE Chachapoyas; 2 = Amazonas: 28 km SSW Leimebamba; 3 = Amazonas: Pomacochas (Florida). Liver and muscle tissues were removed from animals freshly killed using a 10% solution of benzocaine. Tissues were frozen immediately in liquid nitrogen for transport to the laboratory, were stored at -70°C, and were used within 1 yr of collection.

Electrophoretic techniques and data analysis follow Wiens and Titus (1991). Liver and skeletal muscle were homogenized separately with a teflon homogenizer in a 1:1 (v:v) mixture of tissue and 0.01 M Tris-0.001 M EDTA-0.001 M mercaptoethanol, pH 6.8. Homogenates were centrifuged at 13,446 g for 10 min at 5°C. Tissue samples were run at 5°C on horizontal starch gels composed of 12% hydrolyzed potato starch. Products of the presumptive gene loci were visualized by histochemical staining methods (Harris and Hopkinson, 1976; Selander et al., 1971; Siciliano and Shaw, 1976). Buffer recipes are from Hillis (1985) and enzyme nomenclature follows the recommendations of the International Union of Biochemistry Nomenclature Committee (1984). Loci were numbered from anode to cathode and alleles were labelled *a, b, c*, etc., in order of increasing anodal mobility. Enzymes, loci, tissue sources, and buffer systems are listed in Table 1.

To estimate the evolutionary relationships among the populations of *Telmatobius* sampled, I subjected the allozyme data to parsimony analysis. Methods for phylogenetic analysis of allozyme data currently are controversial, largely because of the problem of dealing with the abundance of intraspecific variation (see Swofford and Berlocher 1987, for a recent review). I prefer direct use of frequencies over strict "presence/absence" treatment of allelic data, as the latter method discards potentially useful information (e.g., presence of an alllele at a frequency of 1% as different from 99%; Swofford and Olsen, 1990) and is highly subject to sampling error (Swofford and Berlocher, 1987). However, the computer algorithm for quantitative parsimony analysis of frequency data (FREQPARS; Swofford and Berlocher, 1987) has a weak tree-searching routine and, therefore, is unlikely to find the shortest tree for larger data sets (Swofford and Berlocher, 1987). As a compromise, I used qualititative ("presence/absence") coding of the data to determine the shortest and near-shortest trees (using the PAUP software package; Swofford, 1990), and then input these topologies into FREQPARS for evaluation.

Table 1.   Enzymes, loci, International Union of Biochemistry Nomenclature Committee numbers, tissue sources and buffer systems.

Enzyme	Locus	IUBNC	Tissue	Buffer
Adenosine deaminase	Ada	3.5.4.4	muscle	TC 7.0
Aspartate aminotransferase	Aat	2.6.1.1	liver	TBE 9.1-NAD
Alcohol dehydrogenase	Adh	1.1.1.1	liver	TBE 9.1-NAD
Glycerol-3-phosphate dehydrogenase	G3pdh	1.1.1.8	liver	TBE 9.1-NAD
Glucose-6-phosphate isomerase	Gpi	5.3.1.9	liver	TBE 9.1-NAD
3-Hydroxyisobutyrate dehydrogenase	Hbdh	1.1.1.31	liver	TBE 9.1-NAD
Isocitrate dehydrogenase	Icdh-2	1.1.1.42	liver	LiOH-NADP
Lactate dehydrogenase	Ldh-1	1.1.1.27	liver	TBE 9.1-NAD
	Ldh-2	1.1.1.27	liver	TBE 9.1-NAD
Malate dehydrogenase	Mdh-2	1.1.1.37	liver	LiOH-NADP
Malic enzyme (NADP-dependent malate	Me-1	1.1.1.40	liver	TC 7.0-NADP
dehydrogenase)	Me-2	1.1.1.40	liver	TC 7.0-NADP
Mannose-6-phosphate isomerase	Mpi	5.3.1.8	muscle	TC 7.0
Peptidase-B	Pep-B-1	3.4.13.11	liver	LiOH-NADP
	Pep-B-2	3.4.13.11	liver	LiOH-NADP
Phosphoglucomutase	Pgm	5.4.2.2	liver	Poulik
Sorbitol dehydrogenase	Sdh	1.1.1.14	liver	TBE 9.1-NAD
Superoxide dismutase	Sod	1.15.1.1	liver	TBE 9.1-NAD
Triosephosphate isomerase	Tpi	5.3.1.1	liver	TBE 9.1-NAD

For the qualitative analysis, electromorphs were coded by considering the locus as the character and the allelic array (combination of alleles present in a terminal taxon) as the character state. Polymorphisms within populations were weighted using the step-matrix option (following Mabee and Humphries, 1993). The appearance of a "new" allele as a polymorphism was given an a priori weight of 0.5, as was the fixation of that allele (or the loss of the plesiomorphic allele). Thus, the transformation between the allelic array *aa* to *ab* would be weighted by 0.5, between *aa* and *cc* by 1.0, between *aa* and *cd* by 1.5, and between *ab* and *cd* by 2.0. The branch-and-bound algorithm (Hendy and Penny, 1982) was used to guarantee finding the shortest tree(s). To avoid considering ambiguously placed character states as support, I checked state assignments to each stem using both

the accelerated transformation (ACCTRAN; Farris, 1970; Swofford and Maddison, 1987) and delayed transformation (DELTRAN; Swofford and Maddison, 1987) optimization routines.

Because there is no evidence that the species examined constitute a monophyletic group within *Telmatobius* (and therefore no appropriate outgroup taxa could be identified), all trees were unrooted. Each population was treated as a separate terminal taxon. Although some of these populations almost certainly do not represent distinct, separately evolving lineages (thus violating a basic assumption of phylogenetic analysis), using them as terminal taxa allowed testing of their relationships without making a priori assumptions about their taxonomic assignment.

To avoid creating or exacerbating nonmonophyletic taxa, assignment of newly described species to genera should be justified based on phylogenetic hypotheses rather than overall similarity and convenience. The problem of generic allocation without reference to phylogeny is particularly evident in *Telmatobius;* numerous species have recently been removed from *Telmatobius* and reassigned to different genera (e.g., Lynch, 1978) and even different tribes (e.g., Cannatella, 1985). In this study, generic assignment is argued using derived characters that unite the new species with the type species of *Telmatobius* (*T. peruvianus* Wiegmann 1835), and is discussed at the end of the Results section. Telmatobiine specimens examined for the purpose of determining generic placement are listed in Appendix II.

In the Species Accounts, descriptions generally follow the format of Trueb (1979). However, diagnoses only distinguish among the species from northern Peru. The three Ecuadorian species were treated by Trueb (1979); *Telmatobius cirrhacelis* and *T. vellardi* have distinctive color patterns, whereas *T. niger* can be distinguished from the northern Peruvian species by its unusual arrangement of nuptial spines. *Telmatobius niger* has small conical spines that are restricted to the dorsal and medial surface of the thumb, with a disjunct patch of spines usually (71% of 11 males) present near the inner margin of the inner palmar tubercle. The *Telmatobius* in the adjacent region of central Peru (the department of Ancash) are being revised by Antonio Salas (MHNSM; in prep.) and all seem to be distinct from the species in northern Peru (pers. obs. and pers. comm.). I assume it unlikely that more geographically distant taxa will be conspecific or potentially confused with the species discussed in this study. Because so little is known about the phylogenetic relationships of the species of *Telmatobius* (and polarities of character states therefore are difficult to determine), species are "diagnosed" in the traditional sense (diagnosis = characterization) and the diagnoses are not restricted to derived character states. Terminology and distribution of ecological life zones are based on Tosi (1960).

RESULTS

EXTERNAL MORPHOLOGY

There are few consistent differences in overall head shape among the species of *Telmatobius* from northern Peru. The shape of the snout (and associated characters) seems to vary continuously within and among the species. In general, the snout is long and sloping in *T. thompsoni* (Fig. 3C), moderately long in *T. brevipes* (Fig. 3A), moderately short in *T. truebae* (Fig. 4A) and *T. degener* (Fig. 3D), short and bluntly rounded in *T. atahualpai* (Fig. 5), *T. colanensis* (Fig. 4C), *T. ignavus* (Fig. 3B), and *T. necopinus* (Fig. 4B), and very short and sloping in *T. latirostris* (Fig. 4D).

Except for *Telmatobius ignavus* and a few (7% of 67 specimens) *T. brevipes*, all *Telmatobius* in northern Peru lack a tympanum, and in *T. ignavus* the tympanum is partially concealed by the supratympanic fold and may be difficult to detect (Fig. 3B). A tympanum occurs as a polymorphism in three populations of *T. brevipes* near the city of Cajamarca.
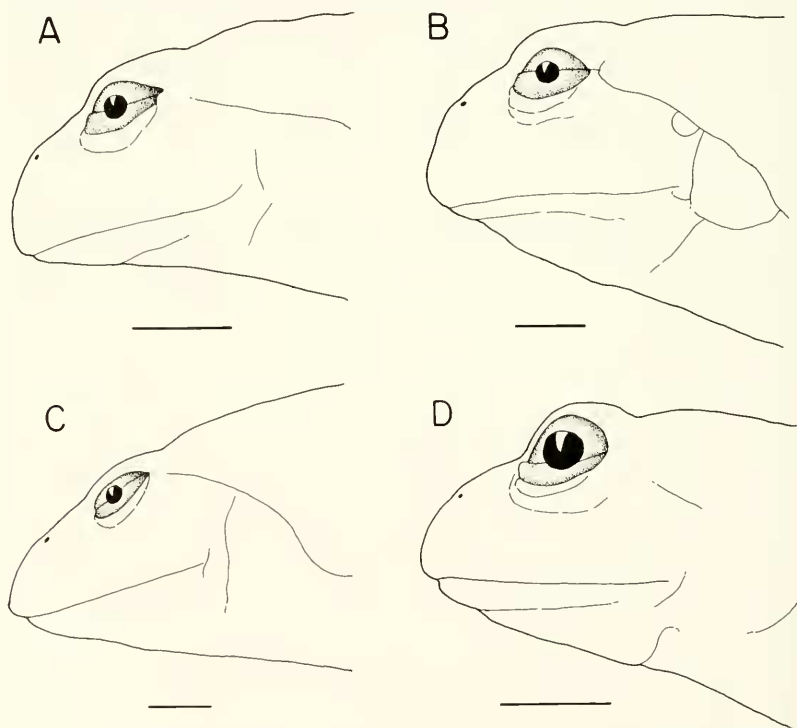

Fig. 3.   Lateral view of heads of *Telmatobius*. **A.** *T. brevipes*, KU 212440. **B.** *T. ignavus*, KU 181442. **C.** *T. thompsoni*, UF 39733. **D.** *T. degener*, UF 39751. Scales = 5 mm.

Palmar supernumerary tubercles are present in *Telmatobius colanensis*, *T. degener*, *T. ignavus*, *T. necopinus*, and *T. thompsoni*, are present in some individuals of *T. brevipes*, *T. latirostris*, and *T. truebae*, and are absent in *T. atahualpai(Figs. 5, 7, 8)*. All specimens of *T. truebae* from Pomacochas (the type locality) are uniquely characterized by having an outer palmar tubercle that is concave at its outer distal margin (in dorsal view); a small supernumerary tubercle is either adjacent to or fused to this concavity (Fig. 8A). Plantar supernumerary tubercles occur in all *T. degener* and in some *T. thompsoni* and *T. truebae*, and are absent in the remaining species. Outer metatarsal tubercles are present in all species, but show considerable inter- and intraspecific variation in size. The outer metatarsal tubercles are con- sistently small and round in *T. necopinus* (about one-fourth size of inner metatarsal tubercle), tend to be small in *T. truebae* (usually about one-third size inner tubercle), and are relatively large in *T. degener* and *T. thompsoni* (about two-thirds to four-fifths size of inner tubercle); in the other species, the outer tubercle is usually about half the size of the inner tubercle. Variation in toe webbing is generally uninformative (see Species Accounts
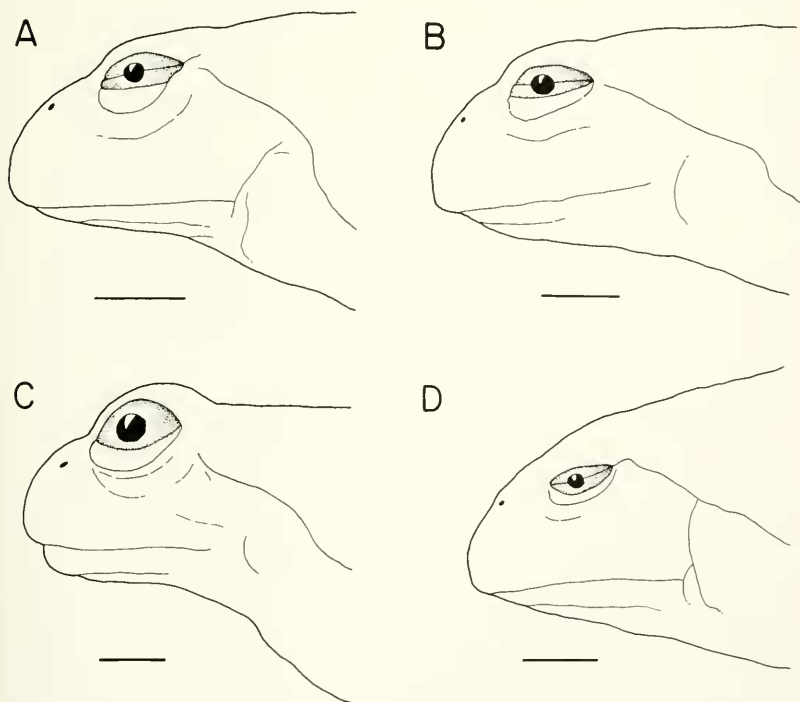

Fig. 4.   Lateral view of heads of *Telmatobius*. **A.** *T. truebae*, KU 181528. **B.** *T. necopinus*, KU 212483. **C.** *T. colanensis*, LSUMZ 37102. **D.** *T. latirostris*, KU 212450. Scales = 5 mm.
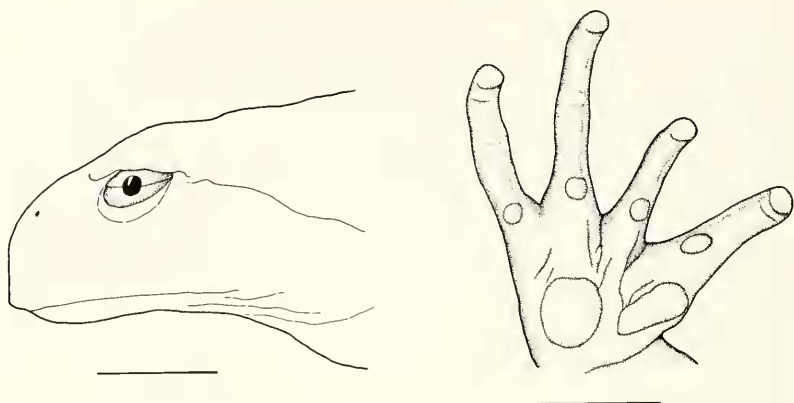
Fig. 5.   Lateral view of head and palmar view of right hand of *T. atahualpai,* UF 39715. Scales = 5 mm.

for webbing formulae of each species), but the toe webbing is relatively extensive in *T. colanensis,* especially between the fourth and fifth toes (Fig. 6).

The size and distribution of keratinized nuptial excrescences on the thumbs of adult males provide invaluable characters for distinguishing among species of *Telmatobius* (Figs. 7–8). *Telmatobius colanensis, T. latirostris, T. necopinus,* and *T. truebae* have large, conical nuptial spines that are restricted to the dorsal and medial surface of the thumb. The slightly raised nuptial pad is distinct from the inner palmar tubercle in each of these species. Among these species, the spines are slightly smaller in *T. colanensis, T. latirostris,* and one of the two male *T. necopinus. Telmatobius degener* also has relatively large, conical spines, but the spines extend onto the ventral surface of the thumb and the nuptial pad is continuous with the inner palmar tubercle. *Telmatobius brevipes, T. ignavus,* and *T. thompsoni* possess minute, close-set nuptial spines. The spines are slightly larger and more distinctly conical in *T. thompsoni* than in *T. brevipes* and *T. ignavus.* The spines are more extensive on the ventral surface of the thumb in *T. brevipes* than in *T. thompsoni,* and are more extensive ventrally in *T. thompsoni* than in *T. ignavus.* In *T. brevipes* and *T. thompsoni,* the swollen nuptial pad obscures the limits of the inner palmar tubercle, whereas in *T. ignavus* the inner palmar tubercle remains distinct.

The dorsum is smooth in *Telmatobius atahualpai, T. degener, T. ignavus, T. necopinus,* and *T. thompsoni,* and usually is smooth in *T. brevipes* (90%; $n = 67$); it usually is coarsely granular in *T. latirostris* and tuberculate in *T. truebae* (82%; $n = 67$). The venter is smooth in all species (pustular near the hindlimbs in male *T. colanensis* and *T. truebae*), but the skin ventromedial to the cloaca usually is pustular in all species except *T. atahualpai.*
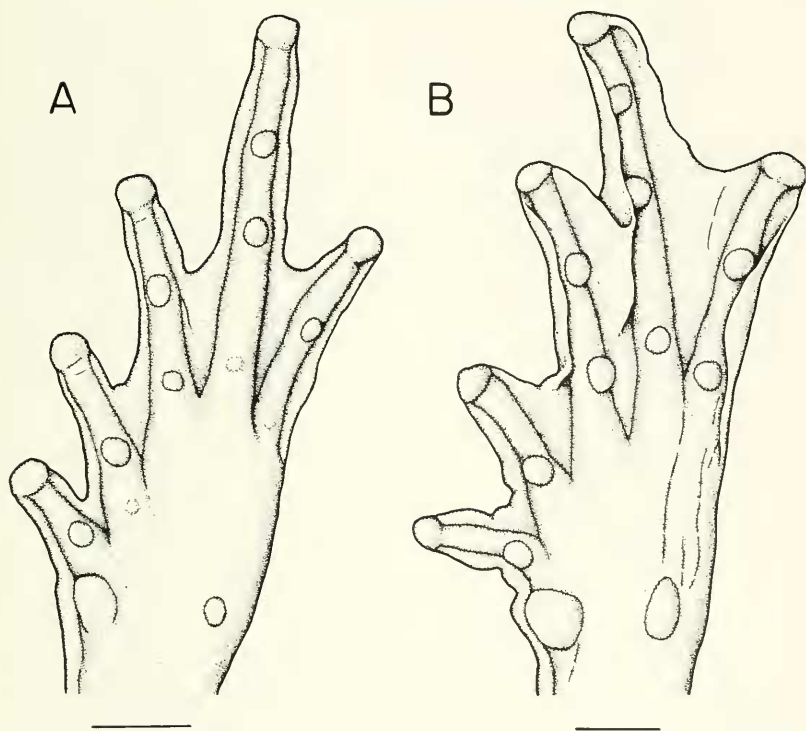
Fig. 6.   Plantar view of left feet of *Telmatobius*. **A.** *T. truebae*, KU 181515. **B.** *T. colanensis*, LSUMZ 37102. Scales = 5 mm.

Photographs of living *Telmatobius atahualpai*, *T. brevipes*, *T. ignavus*, *T. latirostris*, *T. necopinus*, and *T. truebae* are shown in Figure 9. The dorsum is dull brown to gray in *T. brevipes*, *T. ignavus*, *T. necopinus*, and *T. truebae* (in life and preservative) and *T. colanensis*, *T. degener*, and *T. thompsoni* (preservative only, color in life unknown). Darker spots are variably present in these species, and at least one individual of *T. necopinus* had yellowish-tan flecks on the dorsum in life. *Telmatobius latirostris* is unique in having a yellowish-orange dorsum with black spots and reticulations (in life). In living *T. atahualpai*, the dorsum is black with greenish-gold (or metallic green) flecks. The venter and undersides of the limbs are dull gray to tan (in life and preservative) in *T. atahualpai*, *T. colanensis* (color in life unknown), *T. ignavus*, and *T. necopinus*. Bright mottling (yellowish to lavender in life) occurs on the ventral surfaces of the limbs (and sometimes on adjacent parts of the venter) in *T. brevipes* (53%; $n = 67$), *T. latirostris*, and *T. truebae* (90%; $n = 67$). In preserved *T. degener* and *T. thompsoni*, the venter is yellowish cream with gray speckling.
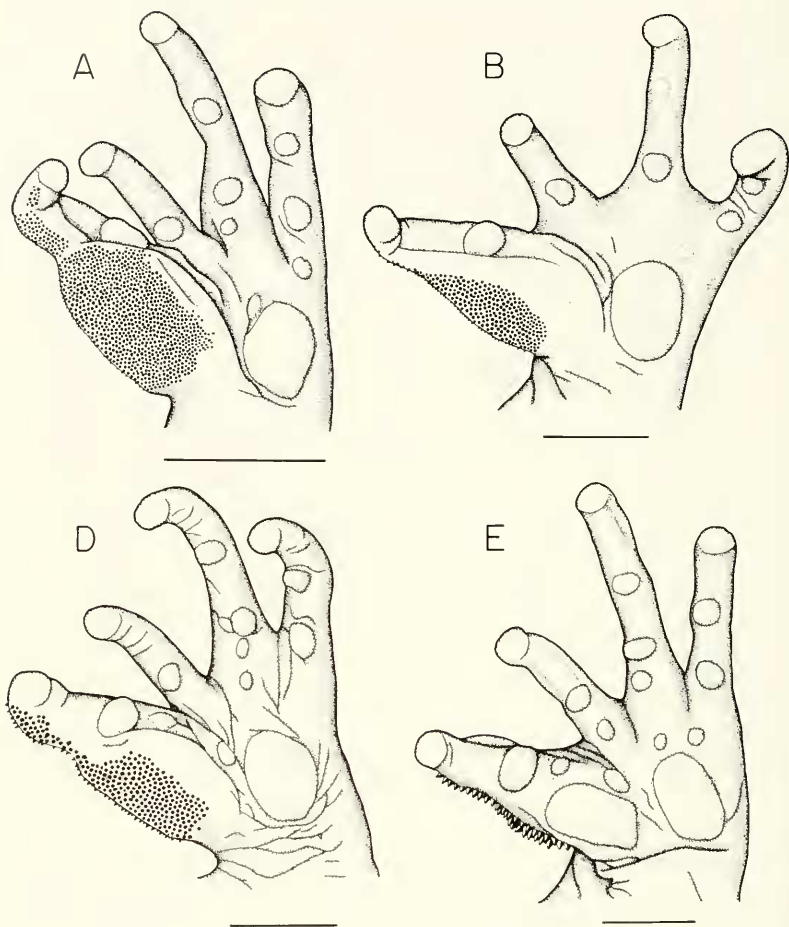
Fig. 7. Palmar view of left hands of male *Telmatobius*. **A.** *T. brevipes*, KU 212435. **B.** *T. ignavus*, UF 34089. **C.** *T. thompsoni*, UF 39734. **D.** *T. latirostris*, KU 212450. Scales = 5 mm.

OSTEOLOGY

The skulls of the seven species for which osteological material is available are illustrated in Figures 10–12. The skull appears relatively wide in *Telmatobius latirostris* (Fig. 11A). The sphenethmoids of *T. degener, T. thompsoni,* and *T. truebae* are poorly ossified and lack the anteromedial ossification between the nasal capsules that is present in adults of the other species. The single adult skeleton of *T. thompsoni* has a small, independent ossification (or mineralization) center within the optic foramen (Fig. 10F); I am not aware of a similar ossification in other anurans. The prootic and
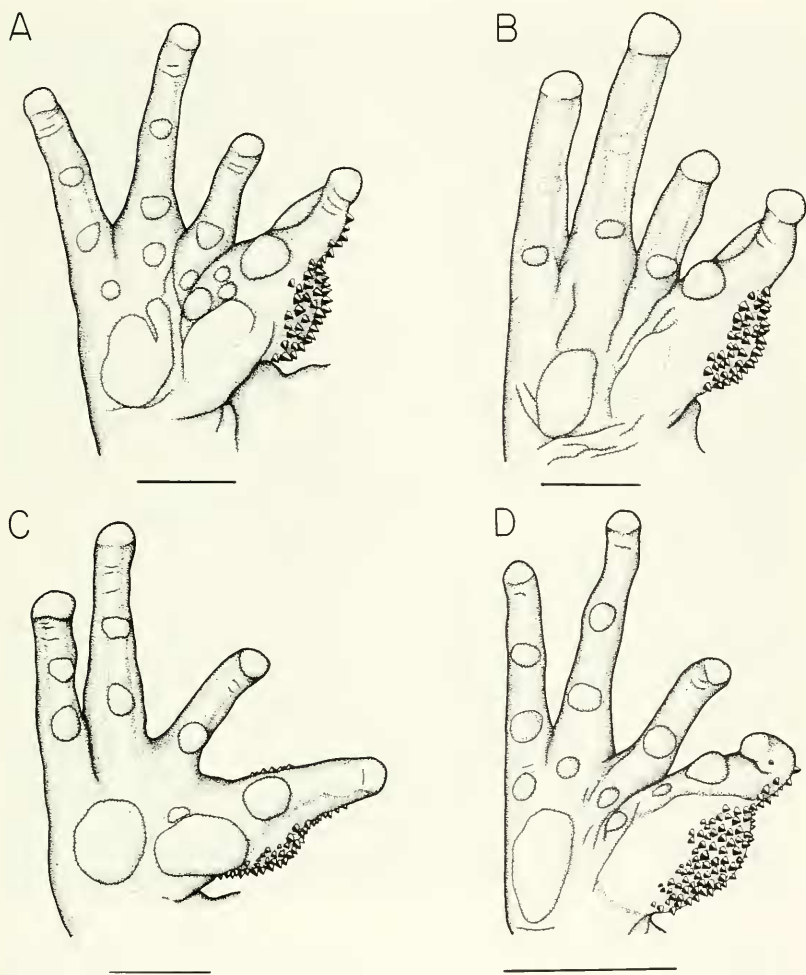
Fig. 8.   Palmar view of right hands of male *Telmatobius*. **A.** *T. truebae*, KU 212476. **B.** *T. necopinus*, KU 212481. **C.** *T. colanensis*, LSUMZ 37102. **D.** *T. degener*, UF 39746. Scales = 5 mm.

exoccipital are fused to each other in adults of all species. The crista parotica is well developed in all species except *T. degener*, in which it is short and unossified (Fig. 12); however, a bony articulation between the squamosal and crista parotica is absent in all species. In *T. degener*, the otic capsules are relatively large (Fig. 12).

The frontoparietals are fused posteriorly in adults of all species (unfused in some individuals of *Telmatobius truebae*) and the frontoparietal fontanelle always is at least partially exposed. The fenestra is most extensive in *T.*

Fig. 9. Photographs of living *Telmatobius*. **Upper left.** Holotype of *T. atahualpai*, subadult female, 43.2 mm SVL, KU 212585. **Upper right.** *T. brevipes*, adult female, 58.0 mm SVL, KU 212413. **Middle left.** *T. ignavus*, juvenile, 39.3 mm SVL, KU 181438. **Middle right.** *T. latirostris*, adult female, 83.6 mm SVL, KU 212448. **Lower left.** Holotype of *T. necopinus*, adult male, 71.4 mm SVL, KU 212482. **Lower right.** Paratopotype of *T. truebae*, adult male, 62.3 mm SVL, KU 212465.

degener, T. necopinus, and *T. truebae*. The nasals are small, slender, and clearly separated medially; in *T. necopinus* the nasals are more slender and curved anteriorly (at midlength) than in the other species (Fig. 11C). Long, slim, palatines (neopalatines of Trueb, 1993) are present in all species (absent on one side of one individual of *T. degener*); the palatines are small and do not reach the maxillae in *T. degener* (Fig. 12B). The lateral end of the palatine is distinctly wider than the medial end in *T. brevipes* (Fig. 10B), whereas the medial end is slightly expanded in *T. thompsoni* (Fig.

10F). The cultriform process of the parasphenoid extends anteriorly to (or almost to) the level of the palatines. The parasphenoid alae are nearly perpendicular to the longitudinal axis of the skull but are slanted slightly posterolaterally. The anterior ramus of the pterygoid extends to the level of the palatines, and overlaps the palatine dorsally. This overlap is most well developed in *T. brevipes* (Fig. 10A). The anterior ramus of the pterygoid bears a distinct dorsal process (presumably for attachment of a ligament from the zygomatic ramus of the squamosal) in *T. thompsoni* and one of the two skeletons of *T. ignavus*. The median ramus of the pterygoid extends to the prootic, but does not abut the parasphenoid ala. In *T. necopinus*, the medial ramus of the pterygoid is especially robust and its articulation with the prootic is expanded (Fig. 11D).

The quadratojugal is present, well developed, and always articulates with the maxilla. The otic ramus of the squamosal is small, and an otic plate is absent. The zygomatic ramus is well developed and deflected medially. The zygomatic ramus is relatively long in *Telmatobius brevipes*, *T. ignavus*, *T. necopinus*, and *T. thompsoni*, moderately short in *T. latirostris* and *T. truebae*, and very short (almost equal in length to the otic ramus) in *T. degener*. *Telmatobius degener* is unique among the species examined in that the jaw articulation is at the level of the crista parotica (Fig. 12), whereas in the other species, the jaw articulation is just posterior to the level of the crista parotica. This difference seems to reflect the relatively short maxillary arch and the more nearly vertical orientation of the ventral ramus of the squamosal in *T. degener*. *Telmatobius latirostris* also has a jaw articulation that is unusually anterior in position (but not as far as in *T. degener*); this may be correlated with the wider skull of this species. The maxillary arcade is dentate in all species except *T. degener*, which lacks teeth on the premaxillae (Fig. 12B). Although loss of teeth on the maxillary arcade has occured in numerous anuran lineages (see Duellman and Trueb, 1986; Trueb, 1973; Trueb, 1993), *T. degener* seems to be the only anuran that lacks premaxillary teeth but retains teeth on the maxillae. The alary processes of the premaxillae are posterodorsally oriented. Typically, the vomers are dentate in all species, but vomerine teeth are absent on one or both sides of some individuals of *T. brevipes*, *T. degener*, and *T. truebae*. The maxillary, premaxillary, and vomerine teeth are elongate, recurved, and fanglike. Little variation was found in mandibular elements, but in *T. necopinus* the posterior margin of the coronoid process of the angulosplenial is concave and recurved; it is convex in the other species.

The columella is present in all species, but its size and shape differ strikingly between and within species and individuals. In most anurans, the columella consists of a long, rodlike stylus laterally and an expanded footplate medially (abutting the operculum). In *Telmatobius brevipes*, this morphology was observed in one of the specimens (KU 180489; Fig. 10B),
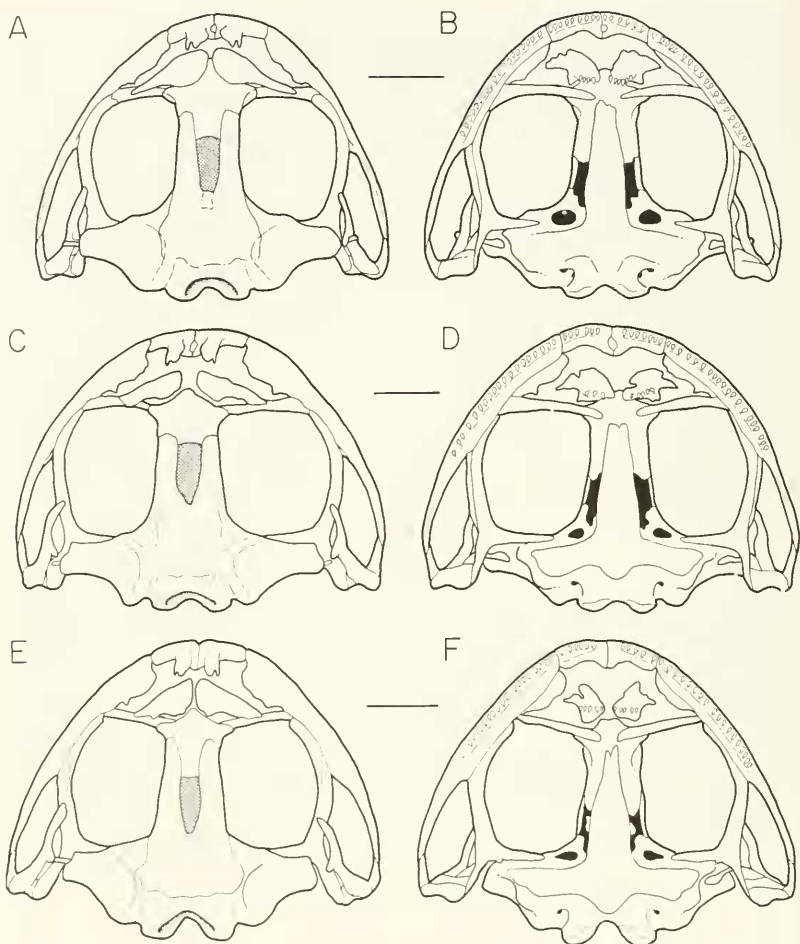
Fig. 10.   Skulls of *Telmatobius* in dorsal (**A, C, E, G**) and ventral (**B, D, F, H**) view. **A–B.** *T. brevipes*, KU 181489. **C–D.** *T. ignavus*, KU 181440. **E–F.** *T. thompsoni*, KU 218468. Septomaxillae and cartilage not shown. Scales = 5 mm.

whereas in another (KU 212447), the stylus is reduced laterally and very thin. In both skeletons of *T. degener*, the columella is reduced to a small, nearly spherical nubbin consisting only of the footplate (Fig. 12B). The columella has the typical shape in the two skeletons of *T. ignavus*, although there is a marked bilateral variation in the thickness of the stylus in one (KU 181441). In the single specimen of *T. latirostris*, the columella is normal on the right side (although unusually thin) and is reduced to a minute, nearly spherical remnant on the left (Fig. 11B). In the exemplar of *T. necopinus* (Fig. 11D), the columella on the left side is slightly shortened
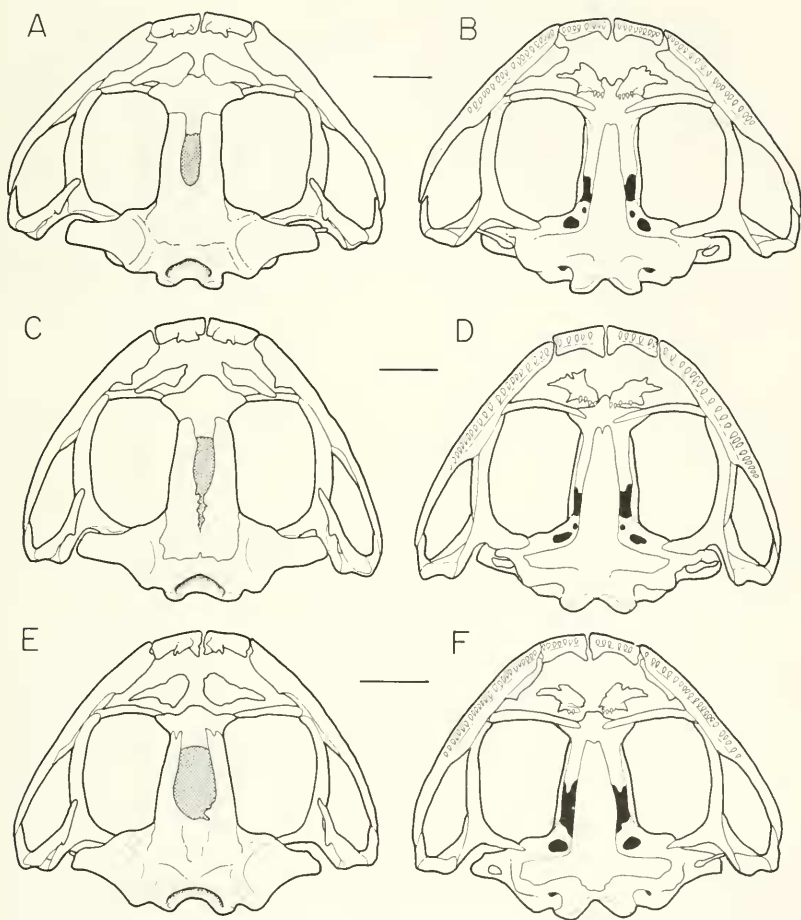
Fig. 11.   Skulls of *Telmatobius* in dorsal view (**A, C, E**) and ventral view (**B, D, F**). **A–B.** *T. latirostris*, KU 212451. **C–D.** *T. truebae*, KU 212464. **E–F.** *T. necopinus*, KU 212184. Septomaxillae and cartilage not shown. Scales = 5 mm.

and dumbell shaped, expanded both laterally and medially. The stylus is absent on the right side in this specimen. The columella is of the usual anuran type on the left side of the adult *T. thompsoni* skeleton (KU 218468; Fig. 10F), on the right side the columella apparently was lost in preparation. The columella morphology is normal on both sides of four of the six skeletons of *T. truebae* observed. In KU 212464 (Fig. 11F), the columella is a spherical nubbin (stylus lost) on the right side; on the left side the stylus is shortened but expanded laterally, and in KU 212478, the columella is shortened on one side. The operculum seems to be present but cartilaginous (sometimes poorly stained) in all species. A tympanic annulus is absent in
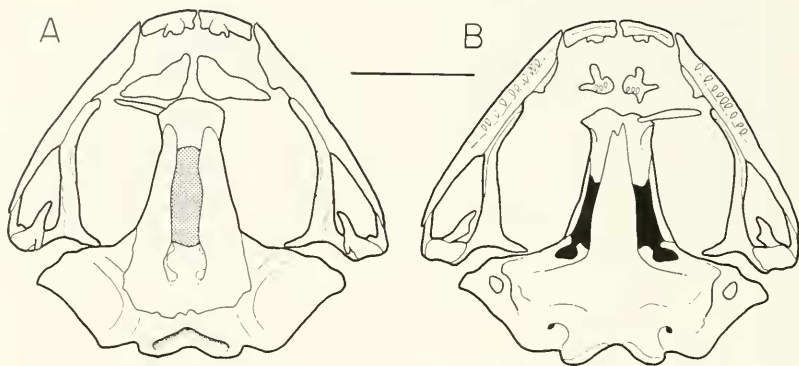
Fig. 12.   Skull of *Telmatobius degener*, KU 218466, in dorsal (**A**) and ventral (**B**) view. Septomaxillae and cartilage not shown. Scale = 5 mm.

T. degener, reduced to one or two sliverlike remnants in *T. necopinus*, and present and complete in the other species. The pars externa plectri seems to be absent in *T. latirostris* (although the tympanic annulus is present) and *T. degener*, but it is present in the other species.

Despite the limited sample sizes, the intraspecific and intraindividual variation in columella morphology observed in these seven species of *Telmatobius* is remarkable. Similarly, Trueb (1979) reported considerable intraindividual variation in presence of the tympannic annulus in 32 specimens of *T. niger* (but she did not determine the condition of the columella). I am unaware of reports of similar levels of intraspecific and bilateral variability in plectral morphology in other anurans. Furthermore, there are few (if any) other anuran groups in which the columella is altered negatively in shape (Trueb, 1985), although it is lost in numerous anuran lineages (including within *Telmatobius*). The extent and source of this apparently unique variation are clearly deserving of further study.

The hyoids of four species (*Telmatobius brevipes*, *T. latirostris*, *T. necopinus*, *T. truebae*) were examined. The hyale bears short, anterior processes in *T. brevipes*, *T. latirostris*, and *T. necopinus* (Fig. 13B). These processes are absent (1 specimen) or are medially oriented (2 specimens) in *T. truebae* (Fig. 13A). An anterolateral hyoid process is present in all four species and usually is distally expanded. Posterolateral processes also are present and are variably expanded distally. The posterolateral processes are short in *T. latirostris* (Fig. 13B). The posteromedial hyoid processes are long and ossified. In *T. latirostris*, ossification of these processes is more advanced on the hyoid plate than in the other species (Fig. 13B) and is accompanied by some calcification of the hyoid plate.

There are eight procoelous, mostly nonimbricate presacral vertebrae. Presacrals I and II are almost imbricate in some individuals (Fig. 14). The
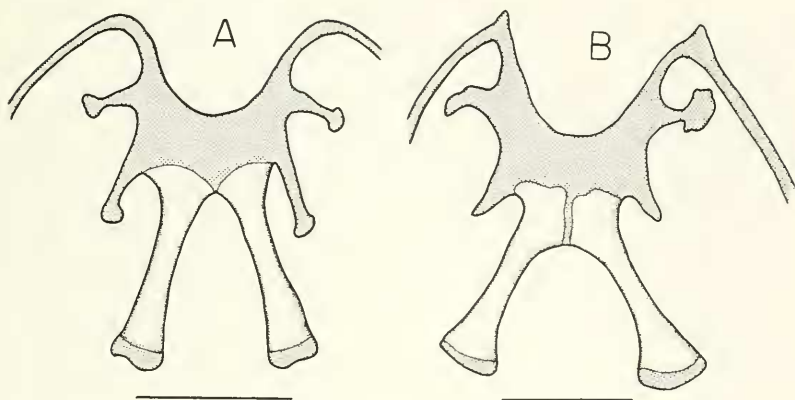
Fig. 13.   Hyoids of *Telmatobius* in ventral view. **A.** *T. truebae*, KU 212480. **B.** *T. latirostris*, KU 212484. Stippled overlay indicates cartilage. Scales = 5 mm.

sacrum and Presacral VIII are fused in the single skeletal preparation of *Telmatobius necopinus*. The transverse processes of the presacral vertebrae are relatively short, thick, and uniform in width in *T. degener* (Fig. 14A). In *T. latirostris* (Fig. 13E), the transverse processes of Presacral II are distinctly curved anteriorly. The atlantal cotyles are relatively narrowly separated (Type II of Lynch, 1971). The sacral diapophyses are slightly dilated, and have a marked dorsolateral orientation in *T. thompsoni*. The urostyle is bicondylar, has a dorsal crest, and usually lacks a lateral flange (present in an apparently aberrant *T. ignavus* and one side of the only skeleton of *T. necopinus*).

The pectoral girdles are fully arciferal, with a cartilaginous sternum that is distinctly notched posteriorly. The omosternum is elongate and cartilaginous. The scapula is bicapitate, and the scapula, coracoid and clavicle are robust and well ossified. The cleithrum is cleft distally into two approximately equal parts. Typically the omosternum, the cartilage of the scapula and suprascapula, and the procoracoid and epicoracoid cartilages are calcified to some degree. The lateral end of the clavicle usually extends to or close to the anterior tip of the pars acromialis of the scapula, but the extent of the clavicle on the scapula is distinctly reduced in *T. necopinus*. Lynch (1978:fig. 15) illustrated the pectoral girdle of *T. brevipes*.

The ilium is cylindrical and bears a moderately well developed crest and dorsal protuberance in all species (Fig. 15). The pubis is ossified in adults of all species (unossified in individuals of *Telmatobius truebae* and *T. degener* of questionable maturity) and is fused indistinguishably with the ilium and ischium; hence, the union of these three elements is indistinguishable in most adults. The acetabular fossa is fully ossified in the best ossified specimen of *T. degener* (Fig. 15D).
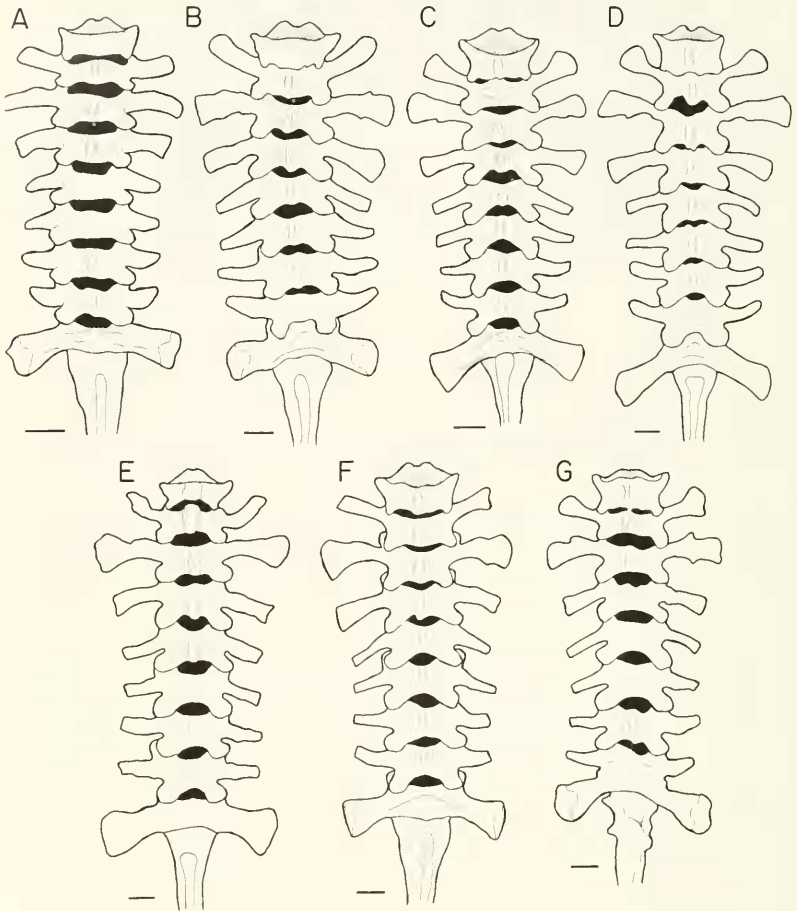
Fig. 14.   Vertebral columns of *Telmatobius* in dorsal view. **A.** *T. degener,* KU 218466. **B.** *T. thompsoni,* KU 218468. **C.** *T. brevipes,* KU 181489. **D.** *T. ignavus,* KU 181440. **E.** *T. latirostris,* KU 212451. **F.** *T. truebae,* KU 181536. **G.** *T. necopinus,* KU 212484. Scales = 5 mm.

The humerus bears distinct posterior and anteroproximal crests (crista medialis and crista ventralis, respectively) in the species for which male skeletons are available (*Telmatobius degener, T. brevipes, T. latirostris,* and *T. truebae*). The crista ventralis is distinctly hypertrophied distally in *T. latirostris.* A small crista ventralis is present on the humerus of females (condition unknown for *T. latirostris*). The hand bears three to five small prepollical elements (with considerable inter- and intraspecific variation); the most distal one to four elements are cartilaginous. There are five other
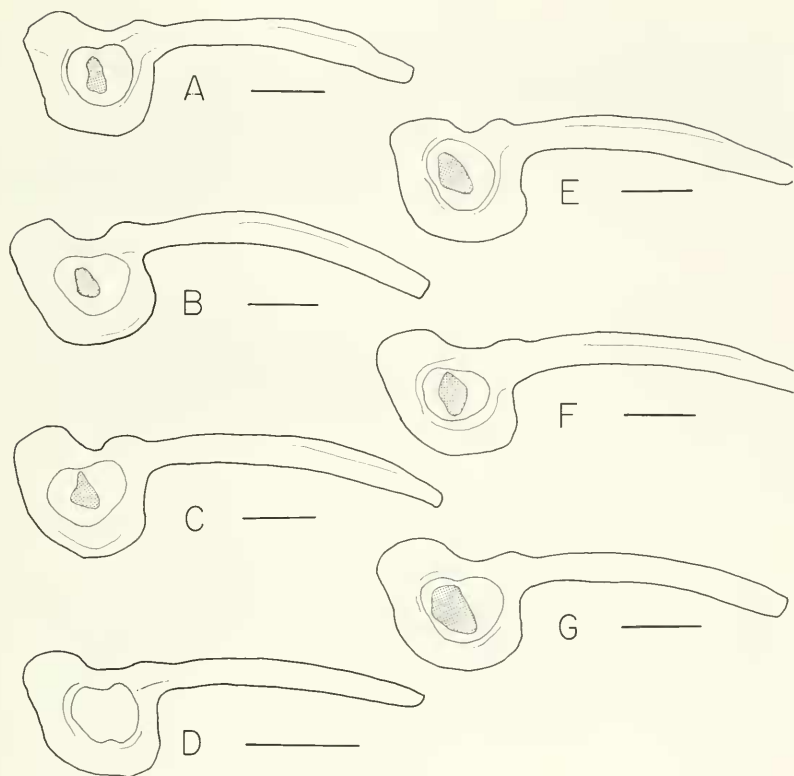
Fig. 15.   Lateral view of pelvic girdles of *Telmatobius*. **A.** *T. brevipes*, KU 181489. **B.** *T. ignavus*, KU 181440. **C.** *T. thompsoni*, KU 218468. **D.** *T. degener*, KU 218466. **E.** *T. latirostris*, KU 212451. **F.** *T. necopinus*, KU 212484. **G.** *T. truebae*, KU 212464. Scales = 5 mm.

carpal elements: the ulnare, radiale, centrale, Carpal 4, and an element consisting of the fused Carpals 2–4. A large sesamoid bone is present dorsal to the radiale in all species. The phalangeal formula of the hand is 2-2-3-3. A bony nuptial tuberosity is present on the medial surface of Metacarpal I in known males; this tuberosity is poorly developed in *T. brevipes*. The foot bears four ossified tarsal elements; an ossified prehallical element (articulating with Metatarsal I), a centrale between the prehallux and fibulare, a small distal tarsal (proximal to Metatarsal II), and a larger distal tarsal (proximal to Metatarsals II–IV). A variable number of small, inconspicuous, usually cartilaginous prehallical elements articulate with the ossified proximal element. The terminal phalanges are knobbed and the phalangeal formula for the foot is 2-3-3-4-3.
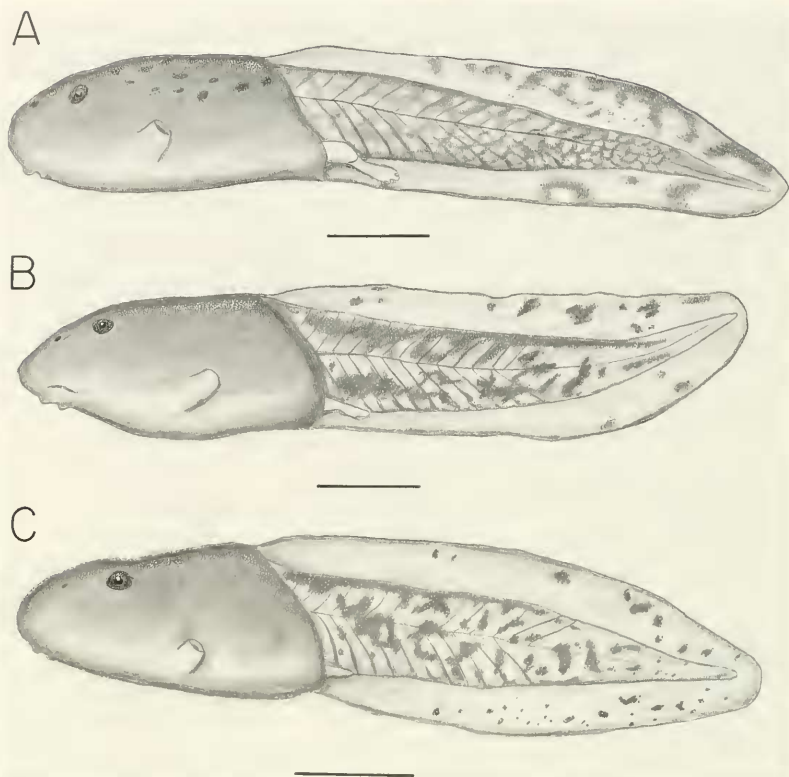
Fig. 16.   Lateral views of tadpoles of *Telmatobius*. **A.** *T. brevipes*, KU 181857 (Stage 38). **B.** *T. ignavus*, KU 181846 (Stage 34). **C.** *T. truebae*, KU 181855 (Stage 35). Scales = 10 mm.

LARVAE

The tadpoles of three species (*Telmatobius brevipes, T. ignavus,* and *T. truebae*) were examined and illustrated (Fig. 16); the following general description applies to all three. The body is ovoid in dorsal and lateral aspects, and is generally more streamlined and less globular in *T. brevipes* than in *T. ignavus* and *T. truebae*. The snout is bluntly rounded in lateral and dorsal profiles. The eyes are dorsolateral and located closer to the laterally oriented nostrils than to each other. The spiracle is lateral and sinistral, and the vent is median. The skin of tadpoles of *T. ignavus* and *T. truebae* often has a loose, "baggy" appearance. The caudal musculature is robust and well developed. The caudal fins do not extend onto the body and the terminus of the tail is blunt. The mouth is anteroventral and the oral disc ovoid. The lateral margin of the oral disc is transangular (vs. constricted; sensu Lavilla, 1988b). Scattered intramarginal papillae are present in the

lateral angular area. Tadpoles of *T. ignavus* have a more extensive prolif- eration of intramarginal papillae laterally than do *T. truebae* and most *T. brevipes;* intramarginal mental papillae are otherwise absent. The marginal labial papillae are broadly interrupted anteriorly. The tooth-row formula is 2/3 and the innermost dorsal and ventral tooth rows are cleft medially. The jaw sheaths are keratinized, wider than high, and the dorsal sheath is wider than the ventral sheath. The inner margins of these sheaths are finely serrated and gently arced. Lavilla (1988b:fig. 1A) illustrated an oral disc typical of *Telmatobius* and the species described here.

In preservative, the dorsum is light brown. Small, round, dark spots are present on the dorsum of most *Telmatobius brevipes* and some *T. ignavus.* The caudal musculature is marbled with brown pigment and the tail fins are transparent and flecked with brown. The caudal musculature of *T. brevipes* is usually more evenly pigmented than in the other species and the caudal fins usually bear more dark pigment. In life, *T. brevipes* is dull olive-tan or green dorsally with or without dark brown spots or greenish flecks (field notes, W. E. Duellman, for KU 181842, 181844, 181857, and 212503). The belly is gray, the tail tan, and the iris dull bronze or brown. The body and caudal musculature of *T. ignavus* are olive-gray; the caudal fins are translu- cent tan and the iris dull bronze (field notes, W. E. Duellman, for KU 181845). In living *T. truebae* tadpoles, the body and caudal musculature are mottled olive-brown with greenish olive and black flecks. The venter is gray and is lavender anteriorly. The fins are translucent tan with dark brown flecks and the iris is pale yellowish bronze (field notes, W. E. Duellman, for KU 181855).

MORPHOMETRICS

Descriptive statistics for the 12 measurements recorded for adult speci- mens of *Telmatobius brevipes, T. degener, T. ignavus, T. latirostris, T. necopinus,* and *T. truebae* are given in Table 2; data for *T. colanensis* and *T. thompsoni* are given in the species descriptions. Aside from differences in size, there are few obvious morphometric differences between the putative species. In order to explore further the morphometric data and to determine if they confirm the groupings based on other kinds of data, I performed a series of multivariate analyses. For these analyses, the species were split into two groups (based on their similarity and geographic proximity) to facilitate differentiation of taxa and interpretation of results. The first group consisted of *T. colanensis, T. latirostris, T. necopinus,* and *T. truebae,* and the second of *T. brevipes, T. degener, T. ignavus,* and *T. thompsoni. Telmatobius atahualpai* was excluded from the morphometric analyses, because thus far, it is known only from sexually immature specimens.

Two sets analyses were performed on each group of species; one ex- plored the morphometric variation independent of taxonomic assignment

Table 2a. Morphometric data for *Telmatobius brevipes*, *T. degener*, and *T. ignavus*. First line is mean ± 1 SD; second line is range. All values are in millimeters; see text for abbreviations of variables.

Character	T. brevipes		T. degener		T. ignavus	
	Males $n = 31$	Females $n = 10$	Males $n = 3$	Females $n = 6$	Males $n = 2$	Females $n = 3$
SVL	52.6 ± 4.76 45.8 –63.5	61.8 ± 5.74 55.0 –71.3	45.3 ± 3.18 42.9 –48.9	43.7 ± 3.01 41.5 –49.6	70.0 ± 7.00 65.0 –74.9	74.6 ± 4.88 69.3 –78.9
TIBL	22.7 ± 1.90 19.8 –29.2	25.1 ± 2.73 22.0 –30.9	22.2 ± 1.87 20.1 –23.7	19.4 ± 1.68 17.3 –21.7	29.9 ± 3.11 27.7 –32.1	31.8 ± 2.40 29.4 –34.2
FOOT	24.5 ± 1.86 21.7 –30.8	27.2 ± 2.58 24.7 –33.7	24.0 ± 2.07 22.1 –26.2	20.1 ± 2.03 17.8 –23.3	32.0 ± 1.77 30.7 –33.2	35.1 ± 2.75 32.9 –38.2
HLEN	15.4 ± 1.14 13.1 –18.1	17.3 ± 1.60 15.2 –19.4	12.6 ± 0.80 11.8 –13.4	12.2 ± 1.33 10.5 –14.5	22.0 ± 3.11 19.8 –24.2	23.6 ± 1.74 22.3 –25.6
HWID	18.6 ± 1.63 15.8 –23.2	21.2 ± 2.81 17.7 –25.3	15.3 ± 1.27 14.3 –16.7	14.5 ± 1.28 13.0 –16.8	28.0 ± 2.48 26.3 –29.8	28.6 ± 1.22 27.8 –30.0
IOD	3.1 ± 0.38 2.4 – 4.2	3.6 ± 0.36 3.1 – 4.1	2.2 ± 0.15 2.1 – 2.4	2.3 ± 0.36 1.8 – 2.8	5.0 ± 1.70 3.8 – 6.2	5.9 ± 0.23 5.6 – 6.0
IND	3.3 ± 0.31 2.8 – 4.3	3.7 ± 0.40 3.3 – 4.5	3.2 ± 0.29 3.0 – 3.5	2.9 ± 0.17 2.7 – 3.1	5.0 ± 0.50 4.7 – 5.4	5.6 ± 0.15 5.5 – 5.8
ENOS	3.2 ± 0.38 2.6 – 4.0	4.0 ± 0.49 3.5 – 4.7	2.9 ± 0.15 2.8 – 3.1	2.5 ± 0.42 2.1 – 3.3	4.9 ± 0.14 4.8 – 5.0	5.3 ± 0.65 4.7 – 6.0
EYE	5.1 ± 0.34 4.4 – 5.8	5.3 ± 0.48 4.3 – 6.0	4.4 ± 0.12 4.3 – 4.5	4.4 ± 0.40 4.0 – 4.9	6.6 ± 0.14 6.5 – 6.7	7.1 ± 0.68 6.3 – 7.6

Table 2a. Continued.

Character	T. brevipes		T. degener		T. ignavus	
	Males $n = 31$	Females $n = 10$	Males $n = 3$	Females $n = 6$	Males $n = 2$	Females $n = 3$
HNDL	13.1 ± 0.98	14.6 ± 1.27	11.1 ± 0.83	10.3 ± 1.01	18.8 ± 1.06	20.9 ± 1.13
	11.6 – 16.2	13.3 – 17.6	10.4 – 12.0	9.1 – 12.1	18.0 – 19.5	20.2 – 22.2
THBL	8.9 ± 0.82	10.3 ± 1.02	7.0 ± 0.40	7.0 ± 0.89	13.1 ± 1.84	14.1 ± 0.31
	7.5 – 10.9	8.5 – 12.4	6.5 – 7.2	6.0 – 8.5	11.8 – 14.4	13.8 – 14.4
RDL	14.6 ± 1.11	16.0 ± 1.78	12.3 ± 0.91	11.1 ± 0.64	20.7 ± 1.27	21.2 ± 0.36
	12.9 – 17.9	14.1 – 18.9	11.5 – 13.3	10.1 – 11.7	19.8 – 21.6	20.8 – 21.5

Table 2b. Morphometric data for *T. latirostris*, *T. necopinus*, and *T. truebae*. First line is mean ± 1 SD; second line is range. All values are in millimeters; see text for abbreviations of variables.

Character	T. latirostris		T. necopinus		T. truebae	
	Males $n = 3$	Females $n = 2$	Males $n = 2$	Females $n = 1$	Males $n = 16$	Females $n = 20$
SVL	78.9 ± 3.53	83.4 ± 0.21	69.2 ± 3.04	72.9	66.2 ± 3.09	72.1 ± 4.09
	76.7 –83.0	83.3 –83.6	67.1 –71.4		58.2 –69.6	65.4 –82.0
TIBL	33.8 ± 1.80	36.8 ± 0.07	33.3 ± 0.57	32.2	30.1 ± 1.55	31.2 ± 1.38
	31.9 –35.5	36.7 –36.8	32.9 –33.7		25.4 –32.5	28.2 –33.0
FOOT	36.2 ± 1.11	40.4 ± 1.06	34.2 ± 0.71	36.8	31.4 ± 1.76	32.7 ± 1.60
	35.0 –37.2	39.7 –41.2	33.7 –34.7		27.7 –36.1	30.0 –35.4
HLEN	23.8 ± 0.76	24.2 ± 0.21	20.9 ± 0.28	21.6	19.2 ± 1.09	20.9 ± 0.79
	23.0 –24.5	24.1 –24.4	20.7 –21.1		15.8 –20.5	19.6 –22.4
HWID	30.3 ± 0.79	32.8 ± 0.50	27.5 ± 0.99	28.0	24.5 ± 1.06	26.2 ± 1.30
	29.7 –31.2	32.5 –33.2	26.8 –28.2		21.8 –26.1	24.2 –29.0
IOD	4.0 ± 0.20	4.4 ± 0.50	5.0 ± 0.21	5.1	4.3 ± 0.24	4.7 ± 0.36
	3.8 – 4.2	4.1 – 4.8	4.8 – 5.1		3.8 – 4.8	4.0 – 5.4
IND	5.7 ± 0.44	5.9 ± 0.14	5.6 ± 0.21	5.3	4.6 ± 0.28	4.8 ± 0.24
	5.2 – 6.0	5.8 – 6.0	5.4 – 5.7		3.8 – 5.0	4.4 – 5.3
ENOS	5.4 ± 0.81	5.6 ± 0.35	4.9 ± 0.42	5.6	4.6 ± 0.32	5.0 ± 0.39
	4.5 – 6.0	5.4 – 5.9	4.6 – 5.2		3.9 – 5.2	4.2 – 5.7
EYE	6.9 ± 0.50	6.8 ± 0.35	6.4 ± 0.35	7.2	5.7 ± 0.38	5.9 ± 0.26
	6.4 – 7.4	6.6 – 7.1	6.2 – 6.7		5.2 – 6.5	5.1 – 6.3

Table 2b. Continued.

Character	T. brevipes		T. degener		T. ignavus	
	Males $n = 31$	Females $n = 10$	Males $n = 3$	Females $n = 6$	Males $n = 2$	Females $n = 3$
HNDL	21.3 ± 0.70 20.6 –22.0	22.9 ± 0.28 22.7 –23.1	19.6 ± 0.07 19.5 –19.6	20.0	17.6 ± 1.16 14.2 –18.9	18.6 ± 0.73 17.5 –20.1
THBL	14.4 ± 0.32 14.0 –14.6	15.2 ± 0.28 15.0 –15.4	13.2 ± 0.42 12.9 –13.5	14.2	12.6 ± 0.61 11.1 –13.5	13.1 ± 0.92 11.9 –15.1
RDL	22.0 ± 1.38 20.5 –23.2	23.2 ± 0.14 23.1 –23.3	21.3 ± 0.42 21.0 –21.6	21.5	19.6 ± 1.40 16.4 –21.9	20.1 ± 0.86 18.8 –22.4

of individuals (thereby allowing for unbiased discovery of groups), whereas the other maximized difference between groups (species) delimited a priori. First, the data were subjected to Principal Components Analysis (PCA). Principal components are linear composite variables, uncorrelated with each other, that explain the maximum amount of variation observed without reference to a priori assessments of group membership.

For morphometric data, the first principal component generally describes differences in size, but there may be size effects in subsequent principal components (Humphries et al., 1981). Several techniques have been developed to deal with the confounding of shape and size. Rohlf and Bookstein (1987) advocated Burnaby's (1966) method as superior for size correction alone, but others (e.g., Humphries et al., 1981; Bookstein et al., 1985) argued that results obtained using Burnaby's technique are difficult to interpret and that "shearing" (Humphries et al., 1981) is therefore preferable. These techniques are described, discussed, and compared by Rohlf and Bookstein (1987). Both techniques were used in this study, but because they yielded nearly identical results in terms of separation of species, I have presented and interpreted the results of the shearing analysis only. Shearing was implemented using SAS code written and provided by Les Marcus. Burnaby's method was performed using a slightly modified version of the SAS code for shearing, as described by Rohlf and Bookstein (1987). Burnaby's technique was used to generate an adjusted data set with between-group size differences effectively held constant; the adjusted data were then subjected to PCA and canonical discriminant analysis. For both techniques, principal components were derived from variance-covariance matrices (as opposed to correlation matrices) and $\log_{10}$-transformed data, following the recommendations of Bookstein et al. (1985).

Scores of individual specimens of the large-spined and eastern species (*Telmatobius colanensis, T. latirostris, T. necopinus,* and *T. truebae*) on the size component, and the sheared second and third principal components were plotted successively against each other. The least overlap of principal component scores among species is seen when the second and third principal components are compared (Fig. 17, top). This scatterplot is almost identical to that for PC I versus PC II for the Burnaby adjusted data (not shown). *Telmatobius colanensis* and *T. latirostris* are separated from *T. necopinus* and *T. truebae* along Sheared Principal Component II (SPC II). The correlation of individual variables with the principal components reveals the relative importance of these variables in accounting for separation along the principal components. These correlations are given by the loadings in Table 3. Interorbital distance, eye diameter, and internarial distance have the highest loadings for SPC II. *Telmatobius colanensis* and *T. latirostris* are well differentiated along SPC III, which has high loadings for interorbital distance, eye diameter, and thumb length. *Telmatobius necopinus* and *T. truebae* are only poorly differentiated.

Fig. 17. Plot of sheared principal component scores (**top**) and canonical discriminant scores (**bottom**) for *Telmatobius colanensis, T. latirostris, T. necopinus,* and *T. truebae.* SPC = sheared principal component. CAN = canonical discriminant axis. The single individual of *T. colanensis* could not be included as a group in the canonical discriminant analysis.

Canonical discriminant analysis creates uncorrelated linear composite variables (discriminant functions) that maximize differences between groups, where group membership of individuals is specified a priori. Analyses were performed with data transformed using Burnaby's technique

Table 3.   Variable loadings for sheared principal components and discriminant function-variable correlations (pooled within-class canonical structure) from principal components analysis and canonical discriminant analysis of *Telmatobius latirostris*, *T. necopinus*, and *T. truebae*.

Variable	Sheared PC II	Sheared PC III	Canonical Axis I	Canonical Axis II
SVL	0.059	−0.070	0.329	−0.239
IOD	0.592	0.509	−0.088	0.447
ENOS	0.175	0.231	0.229	−0.019
EYE	−0.525	0.525	0.476	0.191
INAD	−0.362	0.240	0.536	0.151
HWID	−0.151	0.029	0.569	−0.115
HLEN	−0.118	0.017	0.430	−0.178
HNDL	−0.092	−0.199	0.496	−0.074
THBL	0.068	−0.402	0.321	−0.089
RDL	0.023	−0.281	0.340	0.026
TIBL	−0.140	−0.178	0.394	0.008
FOOT	−0.190	−0.180	0.480	−0.021

(between-group size held constant) and with the data $\log_{10}$-transformed only. The degree of separation of taxa is nearly identical in both analyses, although the relative contribution of different variables to the discrimination can differ. I have chosen to present and interpret the results using the log-transformed data. Canonical discriminant analysis requires that each group contain more than one individual. Therefore, *Telmatobius colanensis* could not be included, but the morphometric distinctness of this species is evident from the PCA. Unlike the PCA, canonical discriminant analysis showed *T. necopinus* and *T. truebae* to be morphometrically distinct. This is evident in the plot of scores for Canonical Axes I and II (Fig. 17, bottom) for the log-transformed data (which is identical to the plot for the Burnaby adjusted data). These two species show separation along both canonical axes. Based on their large values for pooled within-group canonical structure (the correlation between the canonical discriminant function and the original variables, equivalent to loadings in PCA; Table 3), differences in head width, internarial distance, and hand length are most important to separation along Canonical Axis I (CAN I). *Telmatobius latirostris* and *T. truebae* are separated along CAN II, which is influenced most heavily by interorbital distance. Note that some variables have different rankings in separating the same species in PCA versus canonical discriminant analysis; presumably this reflects the different contributions of the variables to overall variance versus between-group variance.

PCA of the western and small-spined species (*Telmatobius brevipes*, *T. degener*, *T. ignavus*, and *T. thompsoni*) is largely unsuccessful in differen-

tiating the species. The plot of sheared PC II versus sheared PC III illustrates the considerable overlap among the scores (Fig. 18, top); plots of size versus the sheared components (not shown) display similar degrees of overlap. The plot of PC I versus PC II for the Burnaby-adjusted data is virtually identical to the plots of the sheared components.
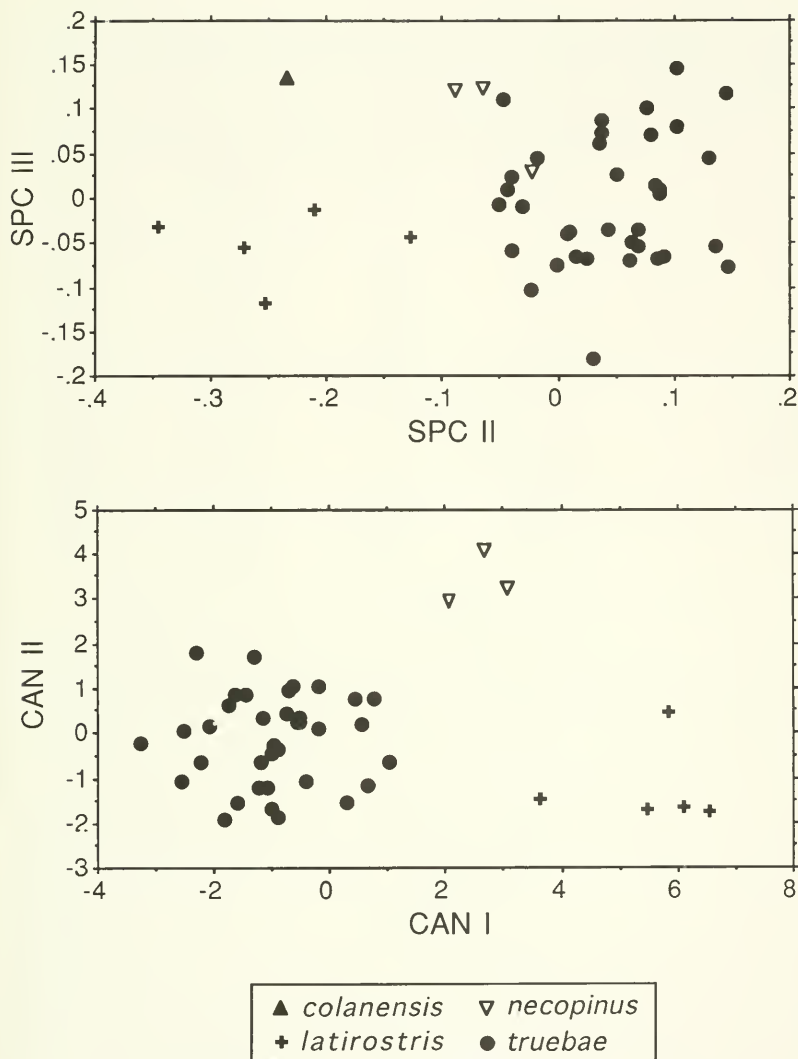

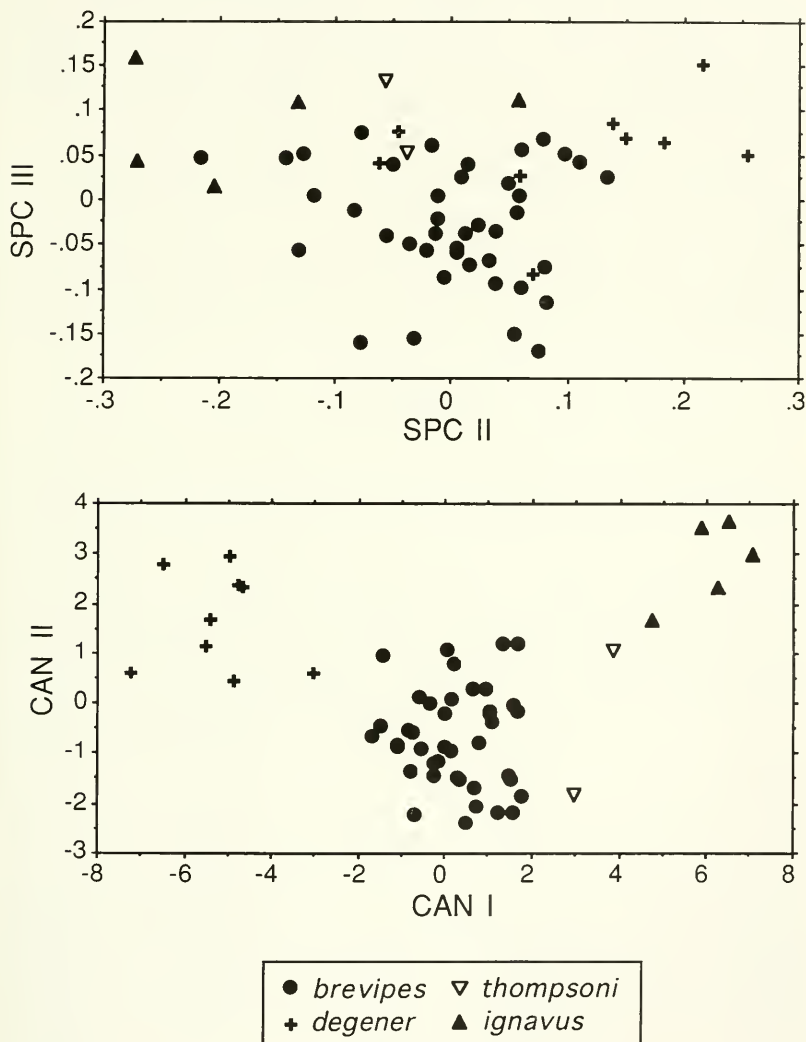Fig. 18. Plot of sheared principal component scores (**top**) and canonical discriminant scores (**bottom**) for *Telmatobius brevipes, T. degener, T. ignavus,* and *T. thompsoni.* SPC = sheared principal component. CAN = canonical discriminant axis.

In contrast, the plot of canonical discriminant scores for the log-trans formed data (Fig. 18, bottom) shows little overlap among the four species. Using Burnaby's technique, the only difference is that there is slightly greater overlap between *Telmatobius brevipes* and *T. thompsoni*. Most of the discrimination occurs along CAN I. Based on the values for canonical structure (pooled within-group, Table 4), the variables that contribute most heavily to discrimination on this axis are hand length, radia length, and head length. Discrimination along CAN II is influenced most strongly by internarial distance, as well as eye diameter and hand length. The large separation between the scores for the two individuals of *T. thompsoni* apparent on CAN II most likely is the result of sexual dimorphism.

In summary, the morphometric data can distinguish among *Telmatobius* species in northern Peru when the groups are determined a priori and differences between them are maximized (using canonical discriminant analysis). Without delimiting groups beforehand (using PCA), little mor phometric differentiation is apparent except among some of the large spined species (*T. colanensis*, *T. latirostris*, *T. necopinus*, *T. truebae*).

Allozymes

Nineteen variable loci were scored (Table 5). These data first were coded qualitatively for phylogenetic analysis (Table 6). Parsimony analysis (using PAUP) yielded two shortest trees (Fig. 19A,B), each with a length of 34 steps. Differences between these trees involve rearrangements of the

Table 4. Variable loadings for sheared principal components and canonical dis criminant function-variable correlations (pooled within-class canonical structure) from principal components analysis and canonical discriminant analysis of *Telmatobius brevipes*, *T. degener*, *T. ignavus*, and *T. thompsoni*.

Variable	Sheared PC II	Sheared PC III	Canonical Axis I	Canonical Axis II
SVL	0.035	0.019	0.440	0.078
IOD	− 0.756	− 0.261	0.559	0.192
ENOS	0.529	− 0.353	0.414	0.162
EYE	− 0.229	0.367	0.523	0.264
INAD	− 0.038	0.661	0.466	0.560
HWID	0.088	0.117	0.576	0.157
HLEN	− 0.022	− 0.016	0.615	0.169
HNDL	− 0.029	0.036	0.632	0.255
THBL	− 0.075	− 0.406	0.536	0.163
RDL	0.007	− 0.034	0.630	0.107
TIBL	0.120	0.180	0.395	0.229
FOOT	0.242	0.143	0.445	0.193

three populations of *Telmatobius truebae*. The optimality (lengths) of these two shortest trees and several near-shortest trees were compared using FREQPARS; there are two trees of 34 steps, four of 34.5 steps, and 17 of 35 steps. Differences among these trees involve rearrangements among the populations of *T. brevipes* and *T. truebae*, and placement of *T. latirostris* with one or more populations of *T. truebae*. Allelic frequencies were calculated from the table of genotypic frequencies (Table 4) and are not presented separately. FREQPARS ranked two of the 23 input trees as shortest, each with a length of 58.08 (Fig. 19A,C). One topology has a length of 34 steps using qualitative character coding (Fig. 19A), whereas the other is 34.5 steps long (Fig. 19C). Differences between these trees involve different placements of populations of *T. brevipes*. In summary, one tree is shortest by both qualitative and quantitative analyses of the electrophoretic data (Fig. 19A). The support for this tree is detailed in Appendix III. However, this particular "phylogeny" of populations within *T. brevipes* and *T. truebae* is chosen somewhat arbitrarily for description; if these populations are interbreeding (reticulating) it may be inappropriate to try to recover (or impose) hierarchical relationships among them.

Several of the morphological characters discussed in previous sections also could support some stems of this tree. *Telmatobius brevipes* (Stem 3) has minute nuptial spines and an extensive nuptial pad that conceals the inner palmar tubercle in males. Both *T. latirostris* and *T. truebae* (Stem 4) have a relatively short zygomatic ramus of the squamosal and usually have tuberculate dorsums and bright mottling on the underside of the limbs, although *T. necopinus* and *T. truebae* tend to have smaller outer metatarsal tubercles. *Telmatobius truebae* (Stem 5) is characterized by a poorly ossi- fied sphenethmoid and processes on the hyale that are medially rather than anteriorly oriented (or are absent). These eight characters were not in- cluded in the parsimony analyses because data are unavailable for popula- tions that were sampled electrophoretically but not osteologically (e.g., *brevipes-1, brevipes-2, truebae-1*) or from which male specimens were not collected (e.g., *truebae-1*); FREQPARS does not work with missing data.

The results of the parsimony analyses of the electrophoretic data show that the populations of *Telmatobius brevipes* and *T. truebae* cluster together in the unrooted tree. Furthermore, all four species examined appear to have at least one "fixed" and "unique" electromorph, although these loci may actually be more variable (if more individuals were sampled) and/or the alleles may diagnose more inclusive groups (if additional species were included).

Population 3 of *Telmatobius brevipes* also seems to have two unique, fixed alleles (Ldh-1[ee], Pep-B-1[dd]). These apparently fixed alleles could suggest that this population is a reproductively isolated lineage that re- quires recognition as a separate species. However, the sample sizes used in

Table 5. Genotypic frequencies at 19 variable loci for nine populations of *Telmatobius. brev* = *T. brevipes*; *latiro* = *T. latirostris*; *necop* = *T. necopinus*; *true* = *T. truebae*. See text for localities of numbered populations. Numbers in parentheses indicate numbers of individuals with each inferred genotype.

Locus	Population								
	brev-1	brev-2	brev-3	brev-4	latiro	necop	true-1	true-2	true-3
Ada	bb (2)	bb (2)	bb (1)	bb (1)	bb (3)	aa (3)	bb (1)	bb (2)	bb (5)
Aat	aa (2)	aa (2)	aa (2)	aa (1)	aa (2)	aa (2)	aa (1)	aa (2)	aa (1); bb (2)
Adh	bb (1); ee (1)	cc (1); ee (1)	ee (1)	aa (1); bb (1)	dd (2)	dd (3)	dd (1)	dd (2)	dd (5)
G3pdh	bb (2)	bb (2)	bb (1)	bb (2)	cc (2)	cc (3)	ac (1)	cc (2)	ac (2); cc (3)
Gpi	aa (2)	aa (2)	aa (1)	aa (2)	aa (2)	aa (3)	bb (1)	bb (2)	bb (5)
Hbdh	cc (2)	ac (1); cc (1)	cc (1)	cc (2)	dd (2)	bb (3)	bb (1)	bb (2)	bb (5)
Icdh-2	bb (2)	bb (2)	bb (1)	bb (2)	aa (2)	aa (3)	aa (1)	aa (2)	aa (5)
Ldh-1	cc (1)	cc (2)	ee (1)	aa (1); cc (1)	cc (3)	cc (2); dd (1)	cc (1)	cc (2)	bb (1); cc (4)
Ldh-2	bb (1)	bb (2)	bb (1)	bb (2)	cc (3)	aa (2); dd (1)	aa (1)	aa (2)	aa (5)
Mdh-2	bb (2)	bb (2)	bb (1)	bb (2)	bb (2)	ab (1); bb (2)	bb (1)	bb (2)	ab (1); bb (4)
Me-1	aa (2)	aa (2)	aa (1)	aa (2)	bb (2)	cc (3)	bb (1)	bb (2)	bb (5)
Me-2	aa (1); bb (1)	bb (2)	ab (1)	ab (1); bb (1)	cc (2)	cc (3)	cc (1)	cc (1); cd (1)	cc (5)

Table 5. Continued.

Locus	Population								
	brev-1	brev-2	brev-3	brev-4	latiro	necop	true-1	true-2	true-3
Mpi	bb (2)	ab (1) bb (1)	bb (1)	bb (1)	cc (3)	cc (3)	cc (1)	cd (1) dd (1)	cc (1) cd (4)
Pep-B-1	aa (1) bb (1)	aa (2)	dd (1)	aa (2)	cc (2)	aa (3)	aa (1)	aa (2)	aa (5)
Pep-B-2	aa (2)	aa (1) dd (1)	aa (1)	aa (2)	bb (2)	cc (3)	aa (1)	aa (2)	aa (5)
Pgm	aa (2)	aa (1) ab (1)	aa (1)	aa (1) bb (1)	bb (2)	aa (2) ab (1)	bb (1)	bb (2)	ab (3) bb (2)
Sdh	bb (1) cc (1)	bb (2)	cc (1)	bb (2)	aa (2)	bb (3)	aa (1)	aa (2)	aa (5)
Sod	aa (1) ab (1)	ab (1) ac (1)	aa (1)	aa (2)	aa (2)	aa (3)	aa (1)	aa (2)	aa (5)
Tpi	aa (2)	aa (2)	aa (2)	aa (1)	aa (2)	aa (3)	ab (1)	aa (2)	aa (3)

the analysis are too small to assess whether or not these alleles are really "fixed" or not and, therefore, whether or not there is gene flow between this population and others. Without additional allozymic data and in the absence of morphological differences between this population and others, I consider it premature to consider this population as a separate species.

The results of the allozyme analysis also demonstrate that, despite their external similarity, *Telmatobius necopinus* and *T. truebae* are not sister taxa. These two species occur in adjacent areas of the Cordillera Oriental and there are no external morphological features that can distinguish them consistently. (All external characters are variable in one or the other species.) This illustrates the potential danger of assigning allopatric populations to a given species on the basis of geographic proximity and/or overall external similarity.

Taxonomic Decisions

In this section, I justify and discuss the recognition of each of the nine evolutionary species of *Telmatobius* in the Andes of northern Peru. *Telmatobius atahualpai, T. degener,* and *T. latirostris* are known from single populations and have unique character states that easily and consistently separate them from their congeners. These are clearly distinct evolutionary lineages, even though *T. atahualpai* is known to date only from subadults.

Telmatobius ignavus is restricted to an isolated mountain range and seems to represent a single interbreeding population. Although similar to *T. brevipes* and *T. thompsoni* (but nevertheless morphologically distinct), the geographical isolation of the Cordillera Huancabamba makes interaction between *T. ignavus* and these species seem extremely unlikely. *Telmatobius thompsoni* is known from a single locality and is similar to, but allopatric with respect to and morphologically distinct from, *T. brevipes* (although there are only two known adults of *T. thompsoni*). Therefore, *T. thompsoni* is also hypothesized to be a distinct lineage, but at this point it is not certain whether the geographical separation (and morphological distinctness) of *T. thompsoni* and *T. brevipes* is real or the result of inadequate sampling.

Because of the allozyme data discussed previously and the absence of obviously derived character states uniting the numerous populations, the status of *T. brevipes* as a single lineage (evolutionary species) is somewhat problematic. Note, however, that the geographical separation of *T. brevipes* into northern and southern groups of populations (apparent in Fig. 1) is not supported by allozymic or morphological data. Assignment of populations to *T. brevipes* was based largely on their morphological and biochemical similarity and geographical proximity to each other—certainly not ideal criteria. However, if there are multiple lineages within *T. brevipes*, their existence and limits are not obvious from data currently available.

Table 6. Data matrix for phylogenetic (PAUP) analysis of nine *Telmatobius* populations (see Table 5 for taxon abbreviations and text for numbered localities) using the following 19 characters: (1) Ada, (2) Aat, (3) Adh, (4) G3pdh, (5) Gpi, (6) Hbdh, (7) Icdh-2, (8) Ldh-1, (9) Ldh-2, (10) Mdh-2, (11) Me-1, (12) Me-2, (13) Mpi, (14) Pep-B-1, (15) Pep-B-2, (16) Pgm, (17) Sdh, (18) Sod, (19) Tpi. Polymorphisms in characters 3, 4, 6, 8–9, and 12–18 were weighted using step matrices. Characters 2, 10, and 19 are polymorphic and were weighted by 0.5.

|	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
brev-1	2:bb	1:aa	2:be	3:bb	1:aa	2:cc	2:bb	2:cc	3:bb	2:bb	1:aa	1:ab	2:bb	2:ab	1:aa	1:aa	3:bc	2:ab	1:aa
brev-2	2:bb	1:aa	3:ce	3:bb	1:aa	1:ac	2:bb	2:cc	3:bb	2:bb	1:aa	2:bb	1:ab	1:aa	2:ad	2:ab	2:bb	3:abc	1:aa
brev-3	2:bb	1:aa	4:ee	3:bb	1:aa	2:cc	2:bb	5:ee	3:bb	2:bb	1:aa	1:ab	2:bb	4:dd	1:aa	1:aa	4:cc	1:aa	1:aa
brev-4	2:bb	1:aa	1:ab	3:bb	1:aa	2:cc	2:bb	1:ac	3:bb	2:bb	1:aa	1:ab	2:bb	1:aa	1:aa	2:ab	2:bb	1:aa	1:aa
latir	2:bb	1:aa	5:dd	2:cc	1:aa	4:dd	1:aa	2:cc	4:cc	2:bb	2:bb	3:cc	3:cc	3:cc	3:bb	3:bb	1:aa	1:aa	1:aa
necop	1:aa	1:aa	5:dd	2:cc	1:aa	3:bb	1:aa	3:cd	2:ad	1:ab	3:cc	3:cc	3:cc	1:aa	4:cc	2:ab	2:bb	1:aa	1:aa
true-1	2:bb	1:aa	5:dd	1:ac	2:bb	3:bb	1:aa	2:cc	1:aa	2:bb	2:bb	3:cc	3:cc	1:aa	1:aa	3:bb	1:aa	1:aa	2:ab
true-2	2:bb	1:aa	5:dd	2:cc	2:bb	3:bb	1:aa	2:cc	1:aa	2:bb	2:bb	4:cd	4:cd	1:aa	1:aa	3:bb	1:aa	1:aa	1:aa
true-3	2:bb	2:ab	5:dd	1:ac	2:bb	3:bb	1:aa	4:bc	1:aa	1:ab	2:bb	3:cc	4:cd	1:aa	1:aa	3:bb	1:aa	1:aa	1:aa
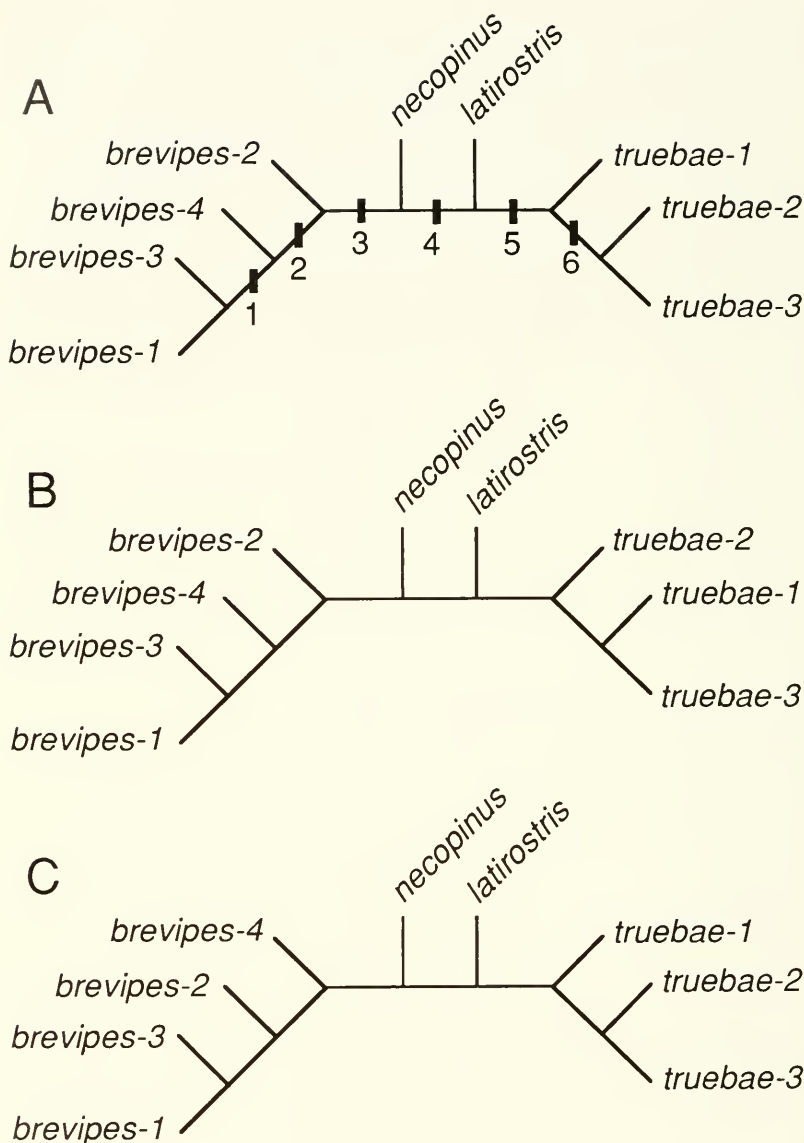
Fig. 19.   Unrooted trees of shortest length from parsimony analysis of allozyme data using PAUP (**A** and **B**; length = 34 steps), and FREQPARS (**A** and **C**; length = 58.08). The support for the numbered stems of Tree A are detailed in Appendix III. The localities of the numbered populations of *Telmatobius brevipes* and *T. truebae* are given in the Materials and Methods; *T. latirostris* and *T. necopinus* are known only from single localities.

The remaining three species (*T. colanensis*, *T. necopinus*, and *T. truebae*) are morphologically distinct from all their congeners in northern Peru and are geographically separated from them (except *T. atahualpai*) by the valley of the Río Marañón. *Telmatobius truebae* presently is known from at least three allopatric populations, whereas *T. colanensis* and *T. necopinus* are each known from single allopatric localities. The distinctness of *T. necopinus* from *T. truebae* is clear from osteology and the allozyme data; they are not sister taxa (see above). There are no apomorphies that unite the populations of *T. truebae* to the exclusion of *T. colanensis*, but there is little variation between the populations of *T. truebae* to suggest that they are separate lineages. Judging by the distribution of cloud forest over 2000 m in the Cordillera Central, it seems reasonable to expect future collecting to show *T. truebae* to be distributed more continuously among the three populations than currently is indicated.

Telmatobius colanensis is considered a distinct evolutionary species because it is allopatric and morphologically diagnosable from the other species. However, discrimination of *T. colanensis* from *T. truebae* and *T. necopinus* is difficult, because only a single specimen of *T. colanensis* exists, the external differences are subtle, and there are no data on its color in life, osteology, larval morphology, or allozymes. Also, the geographical isolation of *T. colanensis* from the other species may be more artifactual than real, as the region is poorly known herpetologically. However, if *T. colanensis* is not a distinct species, it is not clear with which species (*T. necopinus* or *T. truebae*) it is conspecific. Recognition of this specimen as representing a separate species is the best hypothesis given the data at hand.

GENERIC ASSIGNMENT

In this section I discuss evidence for placement of the nine species studied in *Telmatobius*. Unfortunately, no synapomorphies have been proposed to support the monophyly of *Telmatobius*, Telmatobiini, Telmatobinae, or Leptodactylidae. Lynch (1978) performed a cladistic analysis of the so-called "lower telmatobines," a group of doubtful monophyly that includes *Telmatobius*. Certain aspects of Lynch's analysis were clearly problematic (e.g., no outgroups specified). However, for the purposes of this discussion, I accept his hypothesis that *Telmatobius* and *Alsodes* are sister taxa, and note that this arrangement is likely supported by the presence of an enlarged crista medialis on the humerus in males (Lynch's Character 23, not included in his analysis). The recently described genus *Telmalsodes* Díaz 1989 (for *A. montanus* and *A. pehuenche*) is indistinguishable from *Alsodes* and herein is considered a synonym. The only character that purportedly differentiates the two genera is the presence of plantar webbing in *Telmalsodes* (probably plesiomorphic at this level), but plantar webbing also occurs in *Alsodes gargola* (Cei, 1980), *A.*

monticola (pers. obs.), and *A. vanzolinii* (pers. obs.). *Alsodes* (sensu lato) is likely monophyletic based on the presence of paired patches of spines on the chest in males (also in *Insuetophrynus*) and an enlarged crista lateralis on the humerus in males (Lynch, 1978; pers. obs.).

Assuming that *Alsodes* and *Telmatobius* are sister taxa, character states present in both *Alsodes* and other telmatobiine genera are likely to be plesiomorphic in *Telmatobius*. I suggest that assignment of each of the northern Peruvian species (except *T. atahualpai*) to *Telmatobius* is sup ported by two presumptive synapomorphies: (1) frontoparietals fused pos teriorly, and (2) nuptial excrescence on Finger I only. These derived charac ter states are not universal within *Telmatobius*, but because they are shared by the species of interest and the type species of the genus (*T. peruvianus*), they are the ones most relevant to generic allocation. The frontoparietals are fused posterior to the frontoparietal fontanelle in all species of *Telmatobius* for which I have seen skeletal material (Appendix II), except in *T. cirrhacelis* and *T. vellardi*. Frontoparietal fusion is intraspecifically variable in *T. truebae*, *Hylorina sylvatica*, and *Telmatobufo venustus*, but this variation does not endanger the polarity or applicability of this charac ter.

Except for *Telmatobius arequipensis*, all male *Telmatobius* that I have examined (Appendix II) lack a patch of keratinized nuptial excrescences on Finger II. Note that I make a distinction between the patches of spines on Fingers I and II and the small cornified denticles that are widespread on the skin in many telmatobiines. In *Alsodes*, there are distinct nuptial excrescences on both Fingers I and II, but this character is variable among other "lower telmatobiines," with nuptial excrescences present on Finger II in some *Atelognathus* (*A. patagonicus, A. reverberii, A. salai*), *Insuetophrynus, Batrachyla, Caudiverbera,* and *Eupsophus,* but absent in some *Atelognathus* (*A. praebasalticus*), *Hylorina, Lynchophrys,* and *Somuncuria* (the last based on Cei, 1980). *Batrachophrynus* lack nuptial excrescences on both fingers. A rigorous, species-level phylogenetic analy sis is needed to address the monophyly of *Telmatobius*, especially the possible relationship of certain *Telmatobius* to *Lynchophrys* and *Batrachophrynus* (see Cei, 1986; Morales, 1989). Regardless, there is at least some character evidence to support the generic assignment of eight of the species from northern Peru.

Allocation of *Telmatobius atahualpai* is more difficult, as there are no adults, males, or skeletal material available. However, the two larger speci mens have relatively long, recurved, fanglike teeth on the maxilla, premax illa, and vomer. This condition occurs in all *Telmatobius* that I have examined (Appendix II; excepting the edentate *T. carrillae*), but occurs also (to a greater or lesser extent) in *Alsodes* and *Insuetophrynus*. Based on biogeography, it seems more likely that *T. atahualpai* is closely related to

northern Andean *Telmatobius* rather than the Patagonian genera, but this admittedly is not a strong argument. More confident assignment of this species must await the acquisition of additional material.

KEY TO ADULT *TELMATOBIUS* OF NORTHERN PERU

1. Premaxillary teeth present; adult size > 50 mm 2

   Premaxillary teeth absent; adult size < 50 mm ....*T. degener*

2. Dorsum black in life, with yellow-orange reticulations or greenish-gold flecks 3

   Dorsum dull brown to gray in life (with or without darker spots); no yellow-orange reticulations or greenish-gold flecks 4

3. Dorsum black with yellow-orange reticulations; dorsum coarsely granu- lar; skin pustular ventromedial to cloaca; northern Cordillera Occidental ....*T. latirostris*

   Dorsum black (gray to brown in preservative) with greenish-gold flecks; skin smooth; Cordillera Central ....*T. atahualpai*

4. Tympanum present, nuptial spines minute but not extensive on ventral surface of thumb; Cordillera de Huancabamba ....*T. ignavus*

   Tympanum absent (except some *T. brevipes*) 5

5. Nuptial spines minute, extensive on dorsal, lateral, and ventral surface of thumb; nuptial pad continuous with inner palmar tubercle; Cordillera Occidental 6

   Nuptial spines large, conical, restricted to dorsal and lateral surface of thumb; separated from inner palmar tubercle; Cordillera Central 7

6. Nuptial spines larger, less extensive on ventral surface of thumb, larger size (males to 68.9 mm SVL, females 77.3) ....*T. thompsoni*

   Nuptial spines smaller, more extensive on ventral surface of thumb; smaller size (males to 63.5 mm SVL, females 71.3) ....*T. brevipes*

7. Webbing extending to level of ultimate phalange of fifth toe; eyes distinctly protuberant on top of head; inner palmar tubercle with distinct inner margin; inner metatarsal tubercle raised, subcircular; outer metarsal tubercle roughly one-half size of inner; Cordillera Colán ....*T. colanensis*

   Webbing usually not extending to level of ultimate phalange on fifth toe; eye not distinctly protuberant on top of head; inner palmar tubercle with indistinct inner margin; inner metarsal tubercle ovoid; outer metatarsal

tubercle roughly one-third to one-fourth size of inner 8

8. Dorsum usually tuberculate; underside of limbs mottled with yellow to lavender blotches; yellowish-tan flecks absent on dorsum ....*T. truebae*

Dorsum smooth, underside of limbs uniform gray; yellowish-tan flecks present on dorsum in life (in some) ....*T. necopinus*

SPECIES ACCOUNTS

Telmatobius atahualpai new species
Figure 9

Holotype.—KU 212485 a subadult female from the north slope of the Abra Barro Negro, 28 km SSW Leimebamba (7°48' S, 77°51' W), 3470 m, Departamento Amazonas, Peru, collected 23 January 1989 by William E. Duellman.

Paratypes.—KU 182084 from 28.3 km SSW Leimebamba, 3450 m, Departamento Amazonas, Peru, collected 7 March 1979 by William E. Duellman, and UF 39715 from 41 km SW Leimebamba, 3600 m, Amazonas, Peru, collected 27 April 1972 by Fred G. Thompson.

Diagnosis.— (1) Premaxillary teeth present; (2) tympanum absent; (3) condition of nuptial spines unknown; (4) dorsum (in life) black with greenish flecks; (5) venter gray, unpatterned; (6) skin of dorsum smooth; (7) maximum size of adults unknown.

This species is easily distinguished from the other northern Peruvian *Telmatobius* by its unique dorsal coloration. *Telmatobius atahualpai* also can be distinguished from the partially sympatric *T. truebae* by its skin texture and ventral color. The skin of the former species is always smooth, whereas *T. truebae* usually has warts on the dorsum and ventral to the cloaca. In *T. truebae* there is usually (90%) bright yellow to lavender coloration on the underside of the limbs, but in *T. atahualpai* the ventral surfaces are uniform gray.

Description.—(Based on the two largest individuals) head slightly narrower than body; head wider than long (HLEN 77.2–83.9% HWID; $\bar{x} = 80.5 \pm 4.7$, $n = 2$); head length 28.2–28.7% of SVL ($\bar{x} = 28.5 \pm 0.3$, $n = 2$); head width 34.2–36.6% of SVL ($\bar{x} = 35.4 \pm 1.7$, $n = 2$); nostril not protuberant, located at anterior terminus of snout; canthus rostralis indistinct, short, slightly concave in dorsal profile, elevated in lateral profile; loreal region concave; snout short, bluntly rounded; eye anterolateral, protuberant or not on top of head; eye diameter 34.8–37.7% of head length ($\bar{x} = 36.3 \pm 2.0$, $n = 2$); tympanum absent; condition of tympanic annulus unknown; supratympanic fold well developed. Maxillary and premaxillary teeth fanglike, embedded in labial mucosa; dentigerous processes of vomers closer to large, subcircular choanae than to each other; processes medial to

choanae; oriented perpendicular to anteroposterior axis of skull (with slight posteromedial inclination); each process bearing 4–5 ($\bar{x}$ = 4.2, n = 4) fanglike teeth embedded in buccal lining for most of their lengths. Tongue large, subcircular, shallowly notched posteriorly; attached through two-thirds of its length anteriorly, free posteriorly. Condition of vocal slits in males unknown.

Forelimbs relatively slender; dermal wrist fold weakly developed; relative lengths of fingers: III > I ≥ IV > II; webbing and lateral fringes absent; tips of fingers spherical; inner palmar tubercle oval, depressed; outer palmar tubercle slightly larger than outer, subcircular; one round, indistinct subarticular tubercle present proximally on each finger (larger tubercle on Finger I); distal subarticular tubercles barely discernible on Fingers III and IV; supernumerary palmar tubercles absent; condition of nuptial spines unknown. Hind limb length (foot plus tibia) 91.2–94.5% of SVL ($\bar{x}$ = 92.8 ± 2.3, n = 2); relative lengths of toes: V > IV = III > II > I; webbing formula (n = 2): I (2⁻–2)—2½ II 1²⁄₃—(3–3⁺) III (2⁺–2¹⁄₃)—(3²⁄₃– 4⁻) IV (3¹⁄₃–3¹⁄₂)—(1²⁄₃–2)V; webbing diminishing distally to form fringes along lateral margins of toes; tips of toes spherical, approximately equal in size to fingertips; inner metatarsal tubercle distinct, ovoid; outer metatarsal tubercle distinct, subcircular, approximately half size of inner metatarsal tubercle; subarticular tubercles round, mostly distinct, distributed on toes as follows: I(1), II(1), III(2), IV(3), V(2); plantar supernumerary tubercles absent; tarsal fold indistinct extending approximately half length of tarsus, confluent distally with fringe along inner margin of Toe I.

Skin smooth; cloacal opening round, unornamented, at upper level of thigh; transverse fold of skin dorsal to cloacal opening.

Color in preservative: Gray or brown with fine yellow to off-white speckling on face, dorsum, and dorsal surfaces of limbs; slightly paler gray or brown ventrally (with paler speckling on throat, flanks and underside of limbs in KU 212485); tips of fingers and toes yellowish cream; palmar and plantar tubercles pale gray.

Color in life: Dorsum nearly black with metallic green streaks and flecks; venter uniform dark gray (W. E. Duellman field notes for KU 212485). Dorsum black with greenish-gold markings; venter gray; iris dull bronze (W. E. Duellman field notes for KU 212485). Dorsum black with gold flecks (F. G. Thompson field notes for UF 39715).

Measurements of holotype (in mm): SVL: 43.2, TIBL: 18.1, FOOT: 21.3, HLEN: 12.2, HWID: 16.2, IOD: 3.2, IND: 3.3, ENOS: 3.4, EYE: 4.6, HNDL: 11.9, THBL: 7.6, RDL: 12.1.

Distribution.—This species is restricted to the westernmost ridge of the Cordillera Central (Fig. 1) at elevations of 3450–3600 m (Fig. 2).

Ecology.—All specimens were found under rocks by day; KU 212485 was under a rock at the edge of a small stream. Sympatric anurans include

Telmatobius truebae and an undescribed *Eleutherodactylus* of the *unistrigatus* group. Although sympatric with *T. truebae* at the type locality, *T. atahualpai* apparently ranges to slightly higher elevations (to 3600 m) than *T. truebae* (up to 3470 m), whereas *T. truebae* ranges to lower elevations (down to 2180 m) than *T. atahualpai* (to 3450 m). *Telmatobius atahualpai* is found in Very Humid Subalpine Páramo.

Etymology.—The specific name is a patronym of Atahualpa, the last ruler of the Incas, and is a noun in the genitive case.

Telmatobius brevipes Vellard
Figure 9

Telmatobius brevipes Vellard, 1951:71.—Lectotype: MHNSM 3743, from Huamachuco, 3350 m, Departamento La Libertad, Peru.

Diagnosis.— (1) Premaxillary teeth present; (2) tympanum usually (93%) absent; (3) nuptial spines minute, extensive, nuptial pad continuous with inner palmar tubercle; (4) dorsum (in life and preservative) dull brown or gray, usually with darker spots; (5) venter pale brown or gray, underside of limbs frequently (53%) with yellowish color; (6) skin of dorsum usually (90%) smooth; (7) snout-vent length in males to 63.5 mm, in females to 71.3 mm.

The presence of minute nuptial spines on the thumbs of males distinguishes *Telmatobius brevipes* from the other northern Peruvian species, except for *T. ignavus* and *T. thompsoni*. *Telmatobius brevipes* can be distinguished from these two species in the following characters: (1) nuptial spines more extensive on ventral surface of thumb in *T. brevipes*, (2) larger adult size in *T. ignavus* and *T. thompsoni*, (3) anterior ramus of pterygoid substantially overlaps palatine in *T. brevipes*, whereas this process only contacts the palatine in the other two species, and (4) sacral diapophyses with a more dorsal orientation in *T. ignavus* and *T. thompsoni*. *Telmatobius brevipes* also can be distinguished from *T. ignavus* in that in *T. ignavus* the tympanum is always present (usually absent in *T. brevipes*), the quadratojugal is thickened vertically, and the anterior margin of the dorsal lamina of the atlas forms approximately a straight line (indented posteriorly in *T. brevipes*). The body of the tadpole of *T. ignavus* is more globular and less streamlined and the tail is less extensively pigmented. *Telmatobius thompsoni* also can be distinguished from *T. brevipes* in that the nuptial spines are slightly larger, the palatine is more slender laterally than medially (more slender medially in *T. brevipes*), the anterior ramus of the pterygoid bears a distinct raised process, and the sphenethmoid is less extensive.

Description.—Head narrower than body; wider than long (HLEN 75.4–88.3% HWID; $\bar{x} = 82.5 \pm 3.4$, $n = 41$); head length 26.6–32.1% of SVL ($\bar{x}$

= 29.0 ± 1.4, n = 41); head width 30.7–39.9% of SVL ($\bar{x}$ = 35.1 ± 2.1, n = 41); nostril not protuberant, located at anterior terminus of snout; canthus rostralis indistinct, concave dorsally; in lateral profile posteriorly elevated; loreal region concave, slightly depressed; snout long, bluntly rounded in lateral profile; eye oriented anterolaterally, protuberant on top of head; eye diameter 27.7–38.2% of head length ($\bar{x}$ = 32.5 ± 2.7; n = 41); tympanum usually absent (absent in 93% of 67 individuals), tympanic annulus present; supratympanic fold well developed to rudimentary, extending from poste- rior corner of eyelid to insertion of forelimb; vertical fold posterior to corner of jaw weakly developed, if present. Maxillary and premaxillary teeth fanglike, embedded in labial mucosa with only tips protruding; dentigerous processes of vomer closer to small, subcircular choanae than to each other; medial or slightly posterior to choanae; oriented perpendicular to longitudinal axis of skull or with slight posteromedial inclination; each bearing 0–6 ($\bar{x}$ = 2.6, n = 82) recurved, fanglike teeth embedded in buccal lining with only tips portruding. Tongue large, subcircular posterior border free, unnotched or only shallowly notched; tongue attached anteriorly through about two-thirds of its length. Vocal slits absent.

Forelimbs relatively slender, slightly more robust in males; dermal wrist fold weakly developed in males, absent or poorly developed in females; relative lengths of fingers; III > I = IV > II; palmar webbing absent; lateral fringes rudimentary or absent, but well developed lateral fringe present along outer margin of Finger I in males; tips of fingers spherical; in females, inner palmar tubercle approximately elliptical, extending onto proximal portion of Finger I, medial margin usually indistinct; in males, inner palmar tubercle continuous with nuptial pad; outer palmar tubercle distinct, flat, ovoid; one large, round subarticular tubercle present proxi- mally on each finger, tubercle on Finger I very large; smaller, less distinct subarticular tubercles present distally on Fingers III and IV; supernumerary palmar tubercles present or absent proximally on each finger, in some specimens, additional tubercle present along outer margin of inner palmar tubercle; minute, densely packed nuptial spines on dorsal, medial, and ventral surfaces of thumb. Hind limb length (foot plus tibia) 75.0–100.2% of SVL ($\bar{x}$ = 88.6 ± 5.8, n = 41); relative lengths of toes: IV > V = III > II > I; webbing formula (range followed by mode; n = 36): I ($1\frac{1}{2}$–2; $1\frac{2}{3}$)— ($2\frac{1}{3}$–$2\frac{2}{3}$; $2\frac{1}{2}$) II (1–2^-; $1\frac{1}{2}$)—($2\frac{2}{3}$–$3\frac{1}{3}$; 3^+) III ($1\frac{1}{2}$–2^+; 2)—(3^+–$3\frac{2}{3}$; $3\frac{1}{2}$) IV (3–$3\frac{1}{2}$; $3\frac{1}{2}$)—(1^+–2; $1\frac{2}{3}$) V; webbing diminishing distally to form lateral fringes along edges of toes; tips of toes spherical, about equal in size to fingertips; inner metatarsal tubercle small, oval, usually flat, distal edge free; outer metatarsal tubercle subcircular to elliptical, approximately half size of inner metatarsal tubercle; small, round subarticular tubercles dis- tributed on toes as follows: I(1), II(1), III(2), IV(3), V(2); supernumerary plantar tubercles absent; tarsal fold well developed usually extending two-

thirds length of tarsus, confluent distally with fringe along inner margin of Toe 1.

Skin usually smooth dorsally and ventrally; dorsum with small warts in 10% of 67 individuals; skin usually pustular ventral to cloaca; cloacal opening round, unornamented, directed posteriorly at upper level of thighs; thick, transverse fold of skin dorsal to the cloaca in many specimens.

Color in preservative: Face and dorsal surfaces of head, body, and limbs dull brown or gray, with darker markings on dorsum (small flecks to a few large blotches) in most individuals and pale spots in two individuals (KU 212412 and 212429); venter pale brown or gray; ventral surfaces of limbs frequently (53% of 67) yellowish tan, overlain by brown or gray spots (especially medially); yellowish color extending onto entire venter in some individuals; tips of fingers and toes yellowish white; hand and foot tubercles light gray.

Color in life: Dorsum pale to medium olive-green with small to medium-sized dark olive blotches; dorsal surface of thighs with dark flecks (usually) or dark blotches (rarely); posterior surface of thighs light olive; venter greyish olive; chins of smaller individuals with slight yellow tint; iris yellowish green (T. H. Fritts field notes for KU 131684–94 from Huamachuco). Dorsum dull olive-green or tan with darker green or brown spots; lighter tan flecks in some individuals; venter dull cream, olive-cream, or creamy yellow; underside of hind limbs dull yellowish tan or dull orange and gray; iris tan, copper, or bronze with reddish-brown or black reticulations or flecks (W. E. Duellman field notes for KU 212412–24 from various localities in Departamento Cajamarca).

Measurements of lectotype (in mm): SVL 47.6, TIBL 19.8, FOOT 22.5, HLEN 14.0, HWID 16.0, IOD 2.7, IND 3.0, ENOS 2.8, EYE 5.0, HNDL 11.6, THBL 7.7, RDL 12.9.

Larvae.—The following description is based on an individual of Stage 38 from the series KU 181857. The individual is illustrated in Fig. 16A and has the following measurements (in mm): total length 73.4, body length 28.7, basal tail muscle height 8.4, basal tail muscle width 4.9, maximum dorsal fin height 4.4 located 35.7 from body terminus, maximum ventral fin height 3.7 located 29.1 from body terminus, body height 12.1, body width 14.8, eye diameter 2.0, pupil diameter 0.7, interorbital distance 2.8, narial diameter 0.7, internarial distance 3.8, snout-naris 5.6, naris-eye 2.5, transverse oral disc diameter 5.4.

Body ovoid in dorsal and lateral view; snout bluntly rounded; naris small, round, oriented anterolaterally; eyes small, oriented dorsolaterally; spiracular tube lateral, sinistral, located slightly anterior to midlength of body, short, oriented posterodorsally, pigmented only slightly; vent median, unpigmented. Dorsal fin slightly narrower and ventral fin narrower than depth of caudal musculature at midlength of tail; caudal fins not

extending onto body; tail relatively elongate, gradually tapering to blunt terminus; caudal musculature robust. Mouth anteroventral; oral disc ovoid; outer margin of disc pigmented; marginal papillae arranged biserially posteriorly, in single series laterally and anteriorly, unpigmented; anterior gap in marginal papillae wide; oral disc with transangular margin; intramarginal papillae large, present laterally; intramarginal mental papillae absent; jaw sheaths keratinized, gently arced, finely serrated, dorsal sheath wider than ventral; labial tooth row formula 2/3, tooth rows adjacent to jaw sheaths interrupted medially.

Color in preservative: Dorsum of body uniform brown with scattered round, dark brown spots; venter largely unpigmented, intestine visible through skin; caudal musculature evenly covered with brown pigment; dorsal fin with numerous dark blotches scattered throughout its length; ventral fin lightly and irregularly pigmented along ventral margin and terminus.

Color in life: (W. E. Duellman field notes for KU 181857) Body and tail dull olive-tan with dark brown spots; belly grayish white; iris bronze.

Variation: Other individuals included in KU 181857 are generally similar to the specimen described. KU 181843 and 181844 consist of individuals in earlier developmental stages. In life, individuals of KU 181843 were olive-green dorsally and greenish gray below (W. E. Duellman field notes). Tadpoles from Abra Quilsh (26 km NNW Cajamarca, KU 212503) are less streamlined, have a shorter and broader tail, and smaller dark spots on the dorsum. Tadpoles from Abra Comulica (KU 212525) are also less streamlined than those of KU 181857, appear to be slightly larger, are more lightly pigmented, and have only indistinct dark spots on the dorsum. In life, these tadpoles have a silvery-bronze tint on the venter and pale gray fins with black flecks (W. E. Duellman field notes). KU 212526 consists of two tadpoles tentatively assigned to this species (no adults are known from the locality); these individuals are relatively lightly pigmented (especially on the ventral fin) and the dorsum lacks dark brown spots.

Distribution.—*Telmatobius brevipes* is relatively widely distributed in the Cordillera Occidental (Fig. 1) at elevations from 2000–3520 m (Fig. 2).

Ecology.—*Telmatobius brevipes* occurs in or along streams or irrigation ditches in páramo and in cultivated areas. Almost all specimens have been collected by day; most specimens were found under rocks or in streamside vegetation. The distribution is within the Humid and Very Humid Montane Forest (cloud forest) and the Very Humid Subalpine Páramo life zones. Sympatric anurans include *Atelopus peruensis*, *Bufo cophotis*, *B. limensis*, *Gastrotheca peruana*, and *Phrynopus simonsii*. The stomachs of four individuals (KU 131690, 181432, 181435, 212446) contained a planthopper (Homoptera, Membracidae), ants (Hymenoptera, Formicidae), several beetles (Coleoptera: Chrysomelidae, Curculionidae), a springtail

(Collembola, Poduridae), coleopteran larvae (Cantharidae, Elateridae), lepi-
dopteran larvae, a centipede, a nematode, a spider, an earthworm, a slug, a
small, unidentifiable anuran, and an unidentifiable tadpole. Eggs (KU
181842) attributed to this species were found adherent to vegetation in a
narrow rivulet in March. Tadpoles were collected in pools in slow-moving
streams, in grassy ponds, and in irrigation and roadside ditches in January
and March.

Remarks.—Vellard (1951) designated the holotype of *Telmatobius
brevipes* as specimen #3 of the series MHNJP (= MHNSM) 246 (given as
249 by Morales et al., 1990). In the original description, this series con-
tained 13 individuals, of which 246(3) was the largest adult male. When I
examined the type series of this species in 1989, I found that these speci-
mens lacked individual tags and numbers. Two specimens of the original
type series seem to be missing. Comparison of the sizes of the specimens
listed by Vellard (1951) and those of the remaining specimens indicates
that the missing specimens could be Vellard's holotype and allotype (the
largest male and female). Morales et al. (1990) also suggested that the
holotype of this species is missing and listed new numbers for the 11
paratypes (MHNSM 3739–3749). I designate one of these (MHNSM 3743,
the largest male in the series of 11 specimens) as the lectotype of *T.
brevipes*.

Telmatobius colanensis new species

Holotype.—LSUMZ 37102, an adult male, from the Cordillera Colán,
SE La Peca (ca. 5°34' S, 78°19' W), 2410 m, Departamento Amazonas,
Peru, collected 16 October 1978 by Thomas S. Schulenberg.

Diagnosis.— (1) Premaxillary teeth present; (2) tympanum absent; (3)
nuptial spines moderately large, distinctly conical, restricted to dorsal and
lateral surface of thumb and separate from inner palmar tubercle; (4)
dorsum (in preservative) dull gray; (5) venter tan; (6) skin of dorsum
smooth; (7) snout-vent length in male 62.5 mm.

The large size, large nuptial spines, and dull gray dorsum of *T. colanensis*
readily distinguish it from the other species in the region, except for *T.
necopinus* and *T. truebae*. *Telmatobius colanensis* is distinct from these two
species in having: (1) toes more extensively webbed (interdigital webbing
extending to level of ultimate phalange of fifth toe in *T. colanensis,* not
extending as far in *T. necopinus* and *T. truebae*), (2) inner metatarsal
tubercle nearly spherical (vs. elliptical), larger, and more distinctly raised,
(3) outer metatarsal tubercle larger (about one-half size inner vs. about one-
third to one-fourth size inner in *T. necopinus* and *T. truebae*), (4) inner
palmar tubercle with distinct inner margin, and (5) eyes more protuberant
on top of head. *Telmatobius colanensis* can be distinguished further from *T.

truebae in having: (1) skin smooth on dorsum (tuberculate in 82% of *T. truebae*), (2) nuptial spines smaller, and (3) snout usually shorter.

Description.—Head slightly narrower than body; head wider than long (HLEN 78.5% HWID); head length 31.5% SVL; head width 40.2% SVL; nostril not protuberant, located just posterior to anterior terminus of snout; canthus rostralis short, indistinct, and slightly concave in dorsal profile; slightly elevated posteriorly in lateral profile; loreal region concave; snout short, bluntly rounded; eye large, anterolaterally oriented, protuberant on top of head; eye diameter 36.5% of head length; tympanum absent, condition of tympanic annulus unknown; supratympanic fold well developed, smooth. Maxillary and premaxillary teeth fanglike, embedded in labial mucosa; dentigerous processes of vomers closer to small, circular choanae than to each other; located medial to choanae; processes perpendicular to longitudinal axis of skull with slight posteromedial inclination; each bearing five or six recurved, fanglike teeth embedded in buccal lining for most of their lengths. Tongue moderately large, free, and unnotched posteriorly, attached through two-thirds of its length anteriorly. Vocal slits absent.

Forelimbs moderately robust; dermal wrist fold distinct; relative lengths of fingers: III > I > IV > II; palmar webbing absent; weak lateral fringes present on fingers; tips of fingers spherical; inner palmar tubercle oval, distinct; outer palmar tubercle roughly same size as inner, subcircular, slightly raised; one round, distinct subarticular tubercle present proximally on each finger, slightly larger tubercle on Finger I; round subarticular tubercles distally on Fingers III and IV; indistinct supernumerary palmar tubercle proximal to Finger I, adjacent to outer edge of inner palmar tubercle; two smaller, less distinct supernumerary tubercles present proximally on Finger II; tips of fingers roughly spherical; nuptial spines, moderately large, conical, keratinized on dorsal and lateral surface of thumb, spines on raised pad proximally. Hind limb length (foot plus tibia) 102.1% of SVL; relative lengths of toes: IV > III > V > II > I; webbing formula: I $1\frac{2}{3}$—2^+ II $1\frac{1}{3}$—3 III 2—$3\frac{1}{3}$ IV 3—1 V; webbing diminishing distally to form wide fringes along lateral margins of toes; tips of toes spherical, relatively large, roughly equal in size to fingertips; inner metatarsal tubercle ovoid, raised, relatively large; outer metatarsal tubercle subcircular, raised, approximately one half size of inner; subarticular tubercles round, distinct, distributed on toes as follows: I(1), II(1), III(2), IV(3), V(2); supernumerary plantar tubercles absent; tarsal fold extending approximately three-fourths length of tarsus, confluent distally with fringe along inner margin of Toe I.

Skin of dorsum smooth; skin pustular and creased ventromedial to cloaca and on underside of forelimbs; creased on underside of hindlimbs and abdomen; cloacal opening round, unornamented, at upper level of thigh; short transverse fold of skin present dorsal to cloaca.

Color in preservative: Dorsum, dorsal surfaces of limbs, and palmar and plantar surfaces dull gray; venter throat and underside of limbs limbs tan; tips of fingers and toes yellowish tan; palmar and plantar tubercles pale gray. Color in life unknown.

Measurements of holotype: SVL 62.5, TIBL 32.1, FOOT 31.7, HLEN 19.7, HWID 25.1, IOD 3.8, IND 5.1, ENOS 4.3, EYE 7.2, HNDL 16.9, THBL 10.4, RDL 18.6.

Distribution.—Known only from the type locality in the Cordillera Colán (Fig. 1).

Ecology.—Collected in a rocky, high-gradient stream in undisturbed cloud forest (T. Schulenberg, pers. comm.).

Etymology.—The specific name is an adjective formed from the name of the mountain range to which the species is endemic.

Telmatobius degener new species

Holotype.—UF 39736, adult male, collected 13 km ESE Yamobamba, 18 km SE Agallpampa on road from Otuzco to Huamachuco (7°59' S, 78°36' W), Departamento La Libertad, Peru, 3290 m, on 9 May 1972 by Fred G. Thompson.

Paratypes.—KU 218463–66, UF 39738–41, 39743–45, 39748–49, 39752–53, and 39755, same locality and collector as holotype. KU 218466 is a cleared-and-stained skeleton, and KU 218465 is a dry skeletal preparation.

Diagnosis.—(1) Premaxillary teeth absent; (2) tympanum absent; (3) nuptial spines moderately large, distinctly conical, on dorsal and ventral surface of thumb; nuptial pad continuous with inner palmar tubercle; (4) dorsum (in preservative) gray to brown; (5) venter yellowish cream with gray speckling; (6) skin of dorsum smooth; (7) size small; snout-vent length in males to 48.9 mm, in females to 49.6 mm.

This species can be distinguished from the other northern Peruvian *Telmatobius* on the basis of its small size, large, conical, nuptial spines, and the following osteological characters: (1) premaxillary teeth absent, (2) palatine reduced, (3) crista parotica short, (4) otic capsule large, (5) sphenethmoid poorly ossified, (6) jaw articulation at (not posterior to) level of crista parotica, (7) zygomatic ramus of squamosal very short, (8) columella reduced to small spherical nubbin, (9) tympanic annulus and pars externa plectri absent, and (10) transverse processes of posterior presacral vertebrae very short and thick.

Description.—Head equal to or slightly narrower than body; head wider than long (HLEN 79.7–88.0% HWID; $\bar{x} = 83.6 \pm 3.1$, $n = 9$); head length 25.1–29.2% of SVL ($\bar{x} = 27.8 \pm 1.4$, $n = 9$); head width 31.1–34.3% of SVL ($\bar{x} = 33.3 \pm 1.0$, $n = 9$); nostril not protuberant, located at anterior

terminus of snout; canthus rostralis indistinct in dorsal view, slightly el evated in lateral view; loreal region barely concave, slightly depressed; snout short, and rounded in lateral profile, slightly acuminate in dorsal view; margin of upper lip flared slightly; eye anterolaterally oriented; protuberant on top of head; eye diameter 33.1–39.2% of head length ($\bar{x} = 35.4 \pm 2.1$, $n = 9$); tympanum and tympanic annulus absent; supratympanic fold poorly developed. Premaxillary teeth absent; maxillary teeth fanglike, embedded in labial mucosa with tips barely protruding; dentigerous pro cesses of vomers closer to choanae than to each other; anterior to level of choanae; roughly perpendicular to longitudinal axis of skull; each bearing 0–4 ($\bar{x} = 1.9$, $n = 26$) fanglike, recurved teeth; teeth absent on one side of two individuals; teeth embedded in buccal lining for most of their lengths; choana varying from large subcircular opening to small, posterolaterally oriented slit. Tongue large, subcircular, posterior border free, unnotched; attached anteriorly through approximately three-fourths of its length. Vocal slits absent.

Forelimbs moderately robust in males (dermal wrist fold usually present), relatively slender in females (dermal wrist fold absent or rudi mentary); relative lengths of fingers: III > IV ≥ I > II; palmar webbing absent; lateral fringes on fingers absent or rudimentary; tips of fingers spherical; in females, inner palmar tubercle large, raised slightly, extending onto base of Finger I; in males, inner palmar tubercle continuous with nuptial pad; outer palmar tubercle large, ovoid, raised slightly; one large, round subarticular tubercle proximally on each finger; distal subarticular tubercles on Fingers III and IV; one to three supernumerary tubercles proximal to each proximal subarticular tubercle; nuptial spines keratinous, moderately large, distinctly conical, on dorsal and ventral surface of thumb. Hind limb length (foot plus tibia) 85.4–108.4% of SVL ($\bar{x} = 94.2 \pm 7.2$, $n = 9$); relative lengths of toes: IV > III > V > II > I; webbing formula (range followed by mode: $n = 10$): I ($1-1^{1}\!/_{3}$; 1^{+})—($2^{+}-2^{1}\!/_{2}$; $2^{1}\!/_{3}$) II ($1^{+}-1^{1}\!/_{3}$; 1^{+})—($3^{-}-3$; 3) III ($1^{1}\!/_{2}-2^{+}$; $1^{2}\!/_{3}$)—($3-3^{1}\!/_{3}$; 3^{+}) IV ($3-3^{1}\!/_{3}$; 3)—($1-1^{1}\!/_{2}$; 1^{+}) V; webbing diminishing distally to form lateral fringe along edges of toes; tips of toes spherical, roughly equal in size to fingertips; inner metatarsal tubercle large, elliptical, distinctly raised; outer metatarsal tubercle large (two-thirds to four-fifths size of inner metatarsal tubercle), elliptical to ovoid, elevated; subarticular tubercles well developed, round, distributed on toes as follows: I(1), II(1), III(2), IV(3), V(2); row of one to four small supernu merary tubercles present proximally on Toes II–V; tarsal fold distinct, extending approximately two-thirds length of tarsus, confluent distally with fringe along inner margin of Toe I.

Skin smooth dorsally and ventrally; skin pustular ventral to cloaca; cloacal opening round and unornamented, directed posteriorly at upper level of thigh.

Color in preservative: Dorsal surfaces of head and limbs and ventral surfaces of tarsus, forearm, hands, and feet dull gray to brown; venter, throat, underside of limbs, and tips of fingers and toes yellowish cream with gray speckling; hand and foot tubercles pale gray. Color in life unknown.

Measurements of holotype (in mm): SVL 48.9, TIBL 23.7, FOOT 26.2, HLEN 13.4, HWID 16.7, IOD 2.4, IND 3.5, ENOS 3.1, EYE 4.5, HNDL 12.0, THBL 7.2, RDL 13.3.

Distribution.—Known only from the type locality in the Cordillera Occidental (Fig. 1).

Ecology.—According to field notes of F. G. Thompson, the type series was collected in a densely vegetated roadside marsh in an "open pasture." The marsh was fed by a brook draining into the Rio Moche, and was in the Very Humid Subalpine Páramo life zone. The frogs were active and abundant in pools and running water by day (13:30 h), and were found simultaneously with *Telmatobius thompsoni*. The stomach of one individual (KU 218466) contained two caddisfly larvae (Trichoptera; Hydroptilidae and an undetermined family).

Etymology.—The specific name *degener* is a Latin adjective meaning degenerate or departing from its kind, and is used in reference both to the small size and distinctive osteological features of this species.

Telmatobius ignavus Barbour and Noble
Figure 9

Telmatobius ignavus Barbour and Noble, 1920:414.—Holotype: MCZ 4093 (subadult female) from the city of Huancabamba, 2000 m, Departamento Piura, Peru.

Diagnosis.— (1) Premaxillary teeth present; (2) tympanum present; (3) nuptial spines minute, mostly on dorsal and medial surface of thumb; nuptial pad distinct from inner palmar tubercle; (4) dorsum (in life and preservative) dull tan to brown with darker spots; (5) venter tan, gray, or grayish brown; (6) skin of dorsum smooth; (7) snout-vent length in males to 74.9 mm, in females to 78.9 mm.

This species is uniquely characterized among northern Peruvian *Telmatobius* in having a tympanum. A tympanum also is found in some (7%) *T. brevipes*, but *T. brevipes* is distinct in having: (1) nuptial spines more extensive on the ventral surface of the thumb, (2) adult size smaller, (3) anterior ramus of pterygoid with substantial overlap on palatine, (4) quadratojugal more slender, (5) sacral diapophyses more laterally oriented (rather than dorsolaterally), (6) anterior margin of dorsal lamina of atlas posteriorly indented, (7) tadpole body shape more streamlined, and (8) tadpole with caudal fins and musculature usually more extensively pig-

mented. *Telmatobius ignavus* also is similar to *T. thompsoni* in having small nuptial spines, but that species is characterized by (1) snout usually longer, (2) nuptial spines slightly larger, (3) venter yellowish cream with gray speckling (in preservative), (4) palatine more slender laterally, (5) sphenethmoid less extensively ossified anteriorly, and (6) orbitonasal foramen in sphenethmoid large, oblong (vs. small, round foramen in *T. ignavus*).

Description.—Head equal to or slightly narrower than body; head wider than long (HLEN 75.3–85.3% HWID; $\bar{x} = 80.8 \pm 3.6$, $n = 5$); head length 30.4–32.4% of SVL ($\bar{x} = 31.6 \pm 1.0$, $n = 5$); head width 37.0–40.5% of SVL ($\bar{x} = 39.1 \pm 1.5$, $n = 5$); nostril not protuberant, located at anterior terminus of snout; canthus rostralis distinct dorsally, elevated in lateral profile; loreal region concave; snout short, bluntly rounded in lateral profile; eye oriented anterolaterally, somewhat protuberant on top of head; eye diameter 27.7–33.0% of head length ($\bar{x} = 30.1 \pm 2.6$, $n = 5$); tympanum present; tympanic annulus barely visible under skin; tympanum largely concealed posteriorly and dorsally by supratympanic fold; supratympanic fold robust, thick, glandular, extending from posterior corner of eyelid to insertion of forelimb; vertical fold extending ventrally from supratympanic fold to throat, posterior to tympanum and corner of jaw. Maxillary and premaxillary teeth fanglike, embedded in labial mucosa with tips protruding or not; dentigerous processes of vomer approximately equidistant between small, subcircular choanae and each other; processes medial to choanae, perpendicular to longitudinal axis of skull with slight posteromedial orientation; each bearing 2–7 ($\bar{x} = 4.3$, $n = 6$) fanglike, recurved teeth; teeth embedded in buccal lining for most of their lengths. Tongue large, subcircular, posterior border free and shallowly notched, attached anteriorly for approximately two-thirds of its length. Vocal slits absent.

Forelimbs moderately slender; dermal wrist fold absent; relative lengths of fingers: III > I > IV > II; webbing absent; lateral fringes rudimentary or absent; tips of fingers spherical; inner palmar tubercle elliptical, elongate, extending onto Finger I, slightly larger than outer palmar tubercle, distinct from nuptial pad in males; outer palmar tubercle large, ovoid; one large, round subarticular tubercle present proximally on each finger; distal subarticular tubercles on Fingers III and IV; small, indistinct supernumerary palmar tubercle proximal to each proximal subarticular tubercle; tubercle of Finger I situated along outer margin of inner palmar tubercle; nuptial spines minute, keratinous, mostly on dorsal and medial surface of thumb. Hind limb length (foot plus tibia) 82.4–95.2% of SVL ($\bar{x} = 89.3 \pm 4.8$, $n = 5$); relative lengths of toes: IV > III > V > II > I; webbing formula (range followed by mode; $n = 3$): I 2—2½ II (1⅓–1⅔; 1½)—(3–3⅓; 3) III (2–2½; 2⁺)—(3–3½; 3½) IV (3⅓–3½; 3½)—2 V; webbing diminishing distally to form lateral fringes along edges of toes; tips of toes spherical, about equal in size to tips of fingers; inner metatarsal tubercle ovoid,

flat (except in UF 34089); outer metatarsal tubercle oval, slightly raised, one-half to two-thirds size of inner; subarticular tubercles small, round, distributed on toes as follows: I(1), II(1), III(2), IV(3), IV(2); supernumerary plantar tubercles absent; tarsal fold well developed, extending at least two-thirds length of tarsus, confluent distally with fringe along inner margin of Toe I.

Skin of dorsum and venter smooth; skin pustular ventral to cloaca; cloacal opening directed posteriorly at upper level of thighs; opening round and unornamented; transverse fold of skin dorsal to cloaca, usually extending anterolaterally to insertion of hindlimbs.

Color in preservative: Dorsum dull brown or gray; venter lighter brown or gray; tips of fingers and toes yellowish cream; palmar and plantar tubercles pale gray.

Color in life: (for KU 181438–181442, W. E. Duellman field notes) Dorsum dull tan, olive-tan or brown with dark brown, olive-brown, or olive-green spots; venter dull tan, dull gray or grayish brown; iris bronze with black reticulations.

Measurements of holotype (in mm): SVL 54.5, TIBL 23.9, FOOT 26.0, HLEN 17.2, HWID 23.0, IOD 4.5, IND 4.3, ENOS 3.9, EYE 4.7, HNDL 14.5, THBL 10.3, RDL 14.0.

Larvae.—The following description is based on an individual (from the series KU 181846) in Stage 34 (Fig. 16B) with the following measurements (in mm): total length 66.6, body length 28.1, basal tail muscle height 7.6, basal tail muscle width 5.4, maximum dorsal fin height 6.0 located 30.4 from body terminus, maximum ventral fin height 5.1 located 24.3 from body terminus, body height 10.5, body width 16.8, eye diameter 2.0, pupil diameter 0.5, interorbital distance 3.7, narial diameter 0.7, internarial distance 4.4, snout-naris 4.5, naris-eye 2.6, transverse oral disc diameter 6.8.

Body ovoid in dorsal and lateral view; snout bluntly rounded; naris small, round, oriented anterolaterally; eyes small, oriented dorsolaterally; spiracular tube lateral, sinistral, located at about midlength of body, short, opening posterodorsally, lightly pigmented; vent median, short, unpigmented. Dorsal and ventral fins narrower than depth of caudal musculature at midlength; caudal fins not extending onto body; tail tapering to broad, blunt terminus; caudal musculature robust, extending onto body; skin on body loose, baggy. Mouth large, opening ventrally, subterminal; oral disc ovoid; marginal papillae irregularly arranged, at least two papillae thick posteriorly, single row anteriorly and laterally; papillae unpigmented; anterior gap in marginal papillae wide; oral disc with transangular margin; intramarginal papillae present laterally, extending medially for short distance, intramarginal mental papillae absent; jaw sheaths keratinized, gently arced, margins finely serrated; dorsal sheath wider than ventral; labial tooth row formula 2/3; tooth rows adjacent to jaw sheaths interrupted medially.

Color in preservative: Dorsum uniform brown; venter unpigmented, intestine readily visible through skin; caudal musculature with scattered brown pigment; dorsal fin with numerous brown blotches, fewer blotches on ventral fin.

Color in life: (W. E. Duellman field notes) Body and caudal musculature olive-gray; caudal fins translucent tan with gray blotches; iris dull bronze.

Variation: Individuals from El Tambo (KU 181845) are slightly darker in preservative than those closer to Huancabamba (KU 181846–847). In life, tadpoles of KU 181847 (W. E. Duellman field notes) were brown with greenish flecks ventrolaterally; the caudal musculature and fins were tan with gray brown flecks (metallic green flecks proximally on ventral fin) and the iris was greenish bronze.

Distribution.—Known only from the isolated Cordillera Huancabamba (Fig. 1) at elevations from 1840–3080 m (Fig. 2).

Ecology.—Individuals were under rocks in streams by day or in pools by day or night. *Telmatobius ignavus* occurs in Very Humid Montane Forest (most localities), Humid Lower Montane Forest, and possibly Dry Lower Montane Forest (at Huancabamba), and has been found with *Colostethus sylvaticus, Gastrotheca lateonota, Eleutherodactylus cajamarcensis, E. colodactylus, E. cryptomelas, E. rhodoplichus,* at least one undescribed *Eleutherodactylus* (Duellman and Wild), *Phrynopus nebulanastes,* and *P. parkeri.* The stomach of one individual (KU 181441) contained remains of an adult and a larval lepidopteran, two beetles (Coleoptera, Curculionidae), a fly (Diptera, Nematocera), and a larval midge (Diptera, Chironomidae). Tadpoles of this species have been found in both rocky and muddy pools and in rocky streams in January and February.

Remarks.—Duellman and Wild (1993) gave the altitudinal distribution of this species as 2320–3080 m. However, the type locality is at 2000 m (in the city of Huancabamba), and a specimen (UF 52148) has been collected at 1840 m.

Telmatobius latirostris Vellard
Figure 9

Telmatobius latirostris Vellard, 1951:68.—Lectotype: MHNSM 3733, from the city of Cutervo, 2620 m, Departamento Cajamarca, Peru.

Diagnosis.— (1) Premaxillary teeth present; (2) tympanum absent; (3) nuptial spines moderately large, conical; nuptial pad on dorsal surface of thumb and separate from inner palmar tubercle; (4) dorsum (in life) yellow-orange with black spots and reticulations; (5) venter gray (in preservative) with yellowish-cream blotches on underside of limbs; (6) skin of dorsum usually coarsely granular; (7) size large, snout-vent length in males to 83.0 mm, in females to 83.6.

The unique color pattern of *Telmatobius latirostris* readily distinguishes it from congeners. This species also is distinct osteologically in having a wide skull, short posterolateral processes of the hyoid, extensive ossification of the posteromedial hyoid processes onto the hyoid plate, transverse processes of the second presacral vertebrae with a marked anterior curve, and hypertrophy of the distal portion of the anteroproximal (crista ventralis) humeral crest (in males). *Telmatobius latirostris* also is distinct morphometrically from the other large-sized, large-spined species in the region, *T. colanensis*, *T. necopinus*, and *T. truebae*, and is distinct electrophoretically from *T. necopinus* and *T. truebae*.

Description.—Head narrower than body; head wider than long (HLEN 73.5–80.0% of head width; $\bar{x} = 76.7 \pm 2.8$, $n = 5$); head length 28.8–31.1% of SVL ($\bar{x} = 29.8 \pm 0.9$, $n = 5$); head width 37.6–39.9% of SVL ($\bar{x} = 38.8 \pm 0.8$, $n = 5$); nostril not protuberant, located at anterior terminus of snout; canthus rostralis short, indistinct, and concave in dorsal view, elevated in lateral profile; loreal region concave; snout very short, sloping, and bluntly rounded in lateral profile; in dorsal profile bluntly rounded; eye anterolaterally oriented; not protuberant on top of head; eye diameter 26.7–32.2% of head length ($\bar{x} = 28.8 \pm 2.2$, $n = 5$); tympanum absent, tympanic annulus present; supratympanic fold present, robust; extending from posterior corner of eyelid to just anterior to insertion of forelimb; thick vertical fold of skin posterior to corner of jaw, extending from beneath supratympanic fold to throat. Maxillary and premaxillary teeth fanglike; embedded in labial mucosa with only tips protruding; dentigerous processes of vomer slightly closer to each other than to small, subcircular choanae; processes at level with or slightly posterior to choanae; oriented perpendicular to longitudinal axis of skull with posteromedial inclination; each process bearing 3–6 ($\bar{x} = 4.3$, $n = 6$) fanglike, recurved teeth; teeth embedded in buccal lining for most of their lengths. Tongue large, circular, attached anteriorly approximately two-thirds to three-fourths of length; posterior border free and unnotched. Vocal slits absent.

Forelimbs robust in males (dermal wrist fold present), moderately robust in females (dermal wrist fold absent); relative lengths of fingers: III > IV = I > II; webbing absent; lateral fringes usually present along distal margins of fingers, indistinct; tips of fingers spherical; inner palmar tubercle oval, usually equal in size to outer; outer palmar tubercle large, ovoid, slightly depressed; one large, round subarticular tubercle proximally on each finger (tubercle of Finger I very large); distal subarticular tubercles on Fingers III and IV; one or more small supernumerary tubercles present at base of each finger in some individuals; supernumerary palmar tubercle also present along outer, anterior edge of inner palmar tubercle; nuptial pad present on dorsomedial surface of Finger I in males, separate from inner palmar tubercle; nuptial spines moderately large, keratinous, conical,

densely packed, in contact at their bases. Hind limb length (tibia plus foot) 87.2–93.6% of SVL ($\bar{x}$ = 90.2 ± 2.7, n = 5); relative lengths of toes: IV > III ≥ V > II > I; webbing formula (range followed by mode; n = 3): I ($1-1\frac{2}{3}$; 1^+)—($2^+-2\frac{1}{3}$; $2\frac{1}{3}$) II ($1-1^+$; 1)—(3^--3; 3) III ($1\frac{1}{2} -2$; $1\frac{2}{3}$)—($3-3\frac{1}{2}$; 3^+) IV ($3^+-3\frac{1}{3}$; 3^+)—($1\frac{1}{3}-2$; $1\frac{2}{3}$) V; webbing diminishing distally to form lateral fringes along toes; tips of toes spherical, roughly equal in size to tips of fingers; inner metatarsal tubercle ovoid, elevated, large; outer metatarsal tubercle oval, slightly elevated, approximately half size of inner; subarticular tubercles well developed, distributed on toes as follows: I(1), II(1), III(2), IV(3), V(2); plantar supernumerary tubercles absent; tarsal fold distinct, extending approximately one-half to two-thirds length of tarsus, confluent distally with fringe along inner margin of Toe I.

Skin of dorsum usually coarsely granular; skin ventral to cloaca pustular; skin otherwise smooth; cloacal opening round and unornamented, directed posteriorly at upper level of thigh.

Color in preservative: Dorsum, flanks, face, and dorsal surfaces of limbs cream reticulated with black; venter gray; ventral surfaces of limbs and posterior of belly creamy white with dark gray mottling; tips of fingers and toes yellowish white; palmar and plantar tubercles pale gray.

Color in life: Dorsum yellow-orange with black spots and reticulations; iris bronze with fine black reticulation.

Measurements of holotype (in mm): SVL: 76.7, TIBL: 31.9, FOOT: 35.0, HLEN: 23.0, HWID: 29.7, IOD: 3.8, IND: 6.0, ENOS: 4.5, EYE: 7.4, HNDL: 21.3, THBL: 14.5, RDL: 20.5.

Distribution.—Known only from the type locality in the Cordillera Occidental (Fig. 1).

Ecology.—All specimens have been taken in drainage ditches at night inside the city of Cutervo. The vegetation in the immediate area consists of remnant cloud forest along streams, in the Very Humid Montane Forest life zone. *Gastrotheca monticola* and at least one undescribed *Colostethus* also were found in this area.

Remarks.—A similar situation exists for the type material of *Telmatobius latirostris* as was described for *T. brevipes*. Vellard (1951) designated the holotype of *T. latirostris* as specimen #1 of the series MHNJP (= MHNSM) 325, the largest male of a series of 13 specimens. When I examined the type series of this species in 1989, I found 10 specimens in the series, all of which lacked individual tags. One of Vellard's paratypes is now in the Museum National d'Histoire Naturelle (Lavilla, 1988a), thereby leaving two adult specimens unaccounted. Morales et al. (1990) suggested that the holotype and allotype were the missing specimens and listed the remaining 10 specimens as paratypes (new numbers MHNSM 3729–38). I designate the largest male of this series (MHNSM 3733) as the lectotype.

Although I have seen only specimens from Cutervo, John Cadle (pers. comm.) has recently collected this species at other localities in Departamento Cajamarca, and is currently describing the tadpole.

Telmatobius necopinus new species
Figure 9

Holotype.—KU 212482, an adult male from the east slope of the Abra Pardo de Miguel, 39 km ENE Pomacochas (= Florida) on road to Moyobamba (5°46' S, 77°42' W), 2050 m, Departamento Amazonas, Peru, collected 31 January 1989, by John J. Wiens.

Paratypes.—KU 212483 and 212484 (cleared-and-stained skeleton) collected with the holotype, and 212481 collected 1 February 1989, at the same locality.

Diagnosis.— (1) Premaxillary teeth present; (2) tympanum absent; (3) nuptial spines large, conical; nuptial pad on dorsal surface of thumb and separate from inner palmar tubercle; (4) dorsum (in life) dull brown, with yellowish-tan flecks in some; (5) venter olive-gray; (6) skin of dorsum smooth; (7) snout-vent length in males to 71.4 mm, in females to 72.9 mm.

The large size, large nuptial spines, and dull brown dorsum distinguish this species from all other *Telmatobius* in the region except for *T. colanensis* and *T. truebae*. *Telmatobius necopinus* differs from *T. colanensis* in having the eye not protuberant dorsally, less extensively webbed toes, smaller tarsal tubercles, and an indistinct medial margin of the inner palmar tubercle (in males). *Telmatobius necopinus* is difficult to distinguish from *T. truebae* on the basis of external morphology, but differences include: (1) dorsum smooth in *T. necopinus* versus tuberculate in most (82%) *T. truebae*, (2) dorsum with yellowish flecks in some (25%) *T. necopinus*, absent in *T. truebae*, (3) yellow to lavender mottling on underside of limbs in most (90%) *T. truebae*, absent or indistinct in *T. necopinus*, (4) nuptial spines smaller in one of the two males of *T. necopinus*, and (5) metatarsal tubercle always small (about one-fourth size of inner metatarsal tubercle) in *T. necopinus*, usually larger in *T. truebae* (greater than one-fourth inner tubercle in about 70% of adult *T. truebae*). Osteologically, *T. necopinus* is distinct from *T. truebae* in having: (1) nasals more slender and distinctly curved anteriorly at midlength, (2) zygomatic ramus of squamosal longer, (3) median process of sphenethmoid extending between nasals, absent in *T. truebae*, (4) median ramus of pterygoid bent posteriorly and expanded at articulation with prootic, (5) posterior margin of coronoid process of angulosplenial concave, convex in *T. truebae*, (6) tympanic annulus reduced to paired remnants, versus normal and unpaired in *T. truebae*, (7) anteriorly oriented processes on hyale, absent or medially oriented in *T. truebae*, (8) Presacral VIII and sacral vertebrae fused, unfused in *T. truebae*,

and (9) clavicle less extensive on pars acromialis of scapula, lateral end of clavicle extending to tip of pars acromialis in *T. truebae*. *Telmatobius necopinus* and *T. truebae* also are distinct electrophoretically; they share no alleles at five loci (Ada, Gpi, Me-1, Pep-B-2, Sdh) and parsimony analysis of the allozyme data shows they are not sister taxa.

Description.—Head narrower than or as wide as body; head wider than long (HLEN 73.4–78.7% HWID; $\bar{x} = 76.4 \pm 2.7$, $n = 3$); head length 29.0–31.4% of SVL ($\bar{x} = 30.0 \pm 1.3$, $n = 3$); head width 38.4–39.9% of SVL ($\bar{x} = 39.3 \pm 0.8$, $n = 3$); nostril not protuberant; located at anterior terminus of snout; canthus rostralis distinct and slightly concave in dorsal view; elevated in lateral profile; loreal region concave; snout short, obtuse, bluntly rounded in dorsal and lateral view; eye anterolaterally oriented, not protuberant on top of head; eye diameter 30.0–33.3% of head length ($\bar{x} = 31.7 \pm 1.7$, $n = 3$); tympanum absent; tympanic annulus reduced but present; supratympanic fold well developed. Maxillary and premaxillary teeth fanglike, embedded in labial mucosa; dentigerous processes of vomers slightly closer to small, semicircular choanae than to each other, located medial or slightly posterior to choanae; processes perpendicular to longitudinal axis of body with slight posteromedial orientation; each process bearing 3–6 ($\bar{x} = 4.2$, $n = 6$) fanglike teeth; teeth embedded in buccal lining with only tips protruding. Tongue large, subcircular; attached anteriorly for approximately four-fifths of its length; tongue free and unnotched (or shallowly notched) posteriorly. Vocal slits absent.

Forelimbs moderately robust in males, relatively slender in females; weak dermal wrist fold present; relative lengths of fingers: III > I = IV > II; palmar webbing absent; lateral fringes present, extending to tips of fingers; fringe on inner margin of thumb well developed in males; tips of fingers spherical; inner palmar tubercle oval, flat, round, approximately equal in size to outer palmar tubercle; inner margin of tubercle indistinct, continuous with skin of palm; inner palmar tubercle separate from nuptial pad in males; outer palmar tubercle oval, flat; subarticular tubercles small, round, distinct, present proximally on Fingers I–IV; larger tubercle on Finger I; distal subarticular tubercles on Fingers III and IV; one supernumerary palmar tubercle at base of each finger; supernumerary palmar tubercle adjacent to outer anterior margin of inner palmar tubercle small, flat; nuptial spines moderately large (KU 212482) to large (KU 212481), keratinous, conical, on pad on dorsomedial surface of thumb of males. Hind limb length (foot plus tibia) 94.7–99.3% of SVL ($\bar{x} = 96.6 \pm 2.4$, $n = 3$); relative lengths of toes: IV > V ≥ III > II > I; webbing formula (range followed by mode; $n = 3$): I (2^-–2; 2^-)—($2\frac{1}{3}$–$2\frac{1}{2}$; $2\frac{1}{3}$) II ($1\frac{1}{2}$–$1\frac{2}{3}$; $1\frac{2}{3}$)—(3–3^+; 3^+) III (2^+–$2\frac{1}{3}$; $2\frac{1}{3}$)—($3\frac{1}{3}$–$3\frac{2}{3}$; $3\frac{1}{2}$) IV ($3\frac{1}{3}$–$3\frac{2}{3}$; $3\frac{1}{3}$)—($1\frac{2}{3}$–2; 2) V; webbing diminishing distally to form lateral fringes along edges of toes; tips of toes spherical, approximately equal in size to fingertips; inner meta-

tarsal tubercle ovoid, flat; outer metatarsal tubercle small, round, approximately one-fourth size of inner metatarsal tubercle; subarticular tubercles large, round, distributed on toes as follows: I(1), II(1), III(2), IV(3), V(2); plantar supernumerary tubercles absent; tarsal fold well developed, extending approximately two-thirds length of tarsus, confluent distally with fringe of webbing along inner margin of Toe I.

Skin smooth dorsally and ventrally; skin ventral to cloaca pustular; cloacal opening round and unornamented, directed posteriorly at upper level of thigh; transverse fold of skin dorsal to cloacal opening (except KU 212482).

Color in preservative: Dorsum dull brown with numerous minute black flecks and larger dark brown spots; venter pale olive-gray with minute dark flecks (absent in KU 212481), ventral surfaces of limbs, hands, and feet darker gray; tips of fingers and toes off-white; palmar and plantar tubercles pale gray.

Color in life: (W. E. Duellman field notes for KU 212482) Dorsum dull brown with yellowish-tan flecks; venter olive-gray; iris bronze with black reticulations.

Measurements of holotype (in mm): SVL 71.4, TIBL 33.7, FOOT 34.7, HLEN 20.7, HWID 28.2, IOD 5.1, IND 5.4, ENOS 4.6, EYE 6.2, HNDL 19.6, THBL 13.5, RDL 21.6.

Distribution.—*Telmatobius necopinus* is known only from the eastern-most ridge of the Cordillera Central (Fig. 1) at an altitude of 2050 m.

Ecology.—Three specimens were in a muddy roadside ditch at night; the fourth specimen (KU 212481) was under a rock adjacent to a stream by day. The type locality is situated in cloud forest, probably within the Very Humid Lower Montane Forest zone. Other anurans collected at this site include *Scinax oreites, Eleutherodactylus bromeliaceus,* three *Eleutherodactylus* sp., and two undescribed *Colostethus.* The stomach of KU 212484 contained an adult *Colostethus* sp., a large slug, a nematode, an opalione arachnid, two beetles (Coleoptera: Chrysomelidae, Carabidae) and a beetle larva (Hydrophilidae).

Etymology.—A Latin adjective meaning unexpected, referring both to the surprise of finding a *Telmatobius* on the lower Andean slopes and to the unanticipated distinctness of this species, biochemically and osteologically, from the geographically adjacent and externally similar *T. truebae*.

Telmatobius thompsoni new species

Holotype.—UF 39734, adult male, collected 13 km ESE Yamobamba, 18 km SE Agallpampa on road from Otuzco to Huamachuco (7°59' S, 78°36' W), Departamento La Libertad, Peru, 3290 m, on 9 May 1972 by Fred G. Thompson.

Paratypes.—KU 218467, adult female, KU 218468, adult female (dry skeleton), and KU 218469 (cleared-and-stained skeleton; juvenile), UF 39747, 39754, and 39756 (juveniles) same data as holotype.

Diagnosis.— (1) Premaxillary teeth present; (2) tympanum absent; (3) nuptial spines small, distinctly conical, on dorsal and ventral surface of thumb; nuptial pad continuous with inner palmar tubercle; (4) dorsum (in preservative) dull gray or brown with fine speckling of small dark spots; (5) venter dull yellow with small, dull gray or brown spots; (6) skin of dorsum smooth; (7) snout-vent length of males to 68.9 mm, in females to 77.3 mm.

This species is similar to two other species in the region with small nuptial spines, *T. brevipes* and *T. ignavus*. *Telmatobius thompsoni* is unique among these three species in having slightly larger nuptial spines, more slender palatines, and a poorly ossified sphenethmoid. *Telmatobius thompsoni* can be further distinguished from *T. brevipes* in having less extensive proliferation of nuptial spines on the ventral surface of the thumb, a raised process on the anterior ramus of the pterygoid, more dorsal orientation of the sacral diapophyses, and larger size. *Telmatobius ignavus* has a tympanum, a small, round, orbitonasal foramen in the sphenethmoid (vs. large and oblong in *T. thompsoni*), a plain tan to gray venter, and usually has a short, bluntly rounded snout (long and sloping in *T. thompsoni*). This species is also similar to the sympatric *T. degener*, but that species is smaller and lacks premaxillary teeth; the latter character can be assessed without dissection and is consistent in juveniles of *T. thompsoni* as well as adults. *Telmatobius degener* also has larger nuptial spines and differs in several other osteological characters.

Description.—Head equal to or slightly narrower than body; head wider than long (HLEN 73.3–84.4% HWID; $\bar{x}$ = 78.9 ± 7.9, n = 2); head length 28.7–33.1% of SVL ($\bar{x}$ = 30.9 ± 3.1, n = 2); head width 39.2% of SVL (n = 2); nostril not protuberant, located at anterior terminus of snout; canthus rostralis indistinct in dorsal view, not distinctly elevated in lateral profile; loreal region barely concave, depressed; snout long and sloping in dorsal and lateral profile; eye anterolaterally oriented; eye slightly protuberant on top of head; eye diameter 26.8–28.4% of head length ($\bar{x}$ = 27.6 ± 1.1, n = 2); tympanum absent; tympanic annulus present; supratympanic fold moderately well developed, extending from posterior corner of eyelid to anterior to insertion of forelimb; vertical fold of skin posterior to corner of jaw, extending from supratympanic fold to throat. Maxillary and premaxillary teeth fanglike, embedded in labial mucosa with only tips protruding; dentigerous processes of vomers closer to subcircular choanae than to each other, located medial or slightly anterior to choanae; processes oriented laterally, each process bearing 2–6 ($\bar{x}$ = 3.7, n = 6) fanglike teeth embedded in buccal lining for most of their lengths. Tongue large, subcircular, posterior border free and unnotched; attached anteriorly

through about three-fourths of its length. Vocal slits absent.

Forelimb moderately robust in males, less so in females; dermal wrist fold present; relative lengths of fingers: III > IV > I > II; palmar webbing absent; lateral fringes weak or absent; tips of fingers spherical; inner palmar tubercle large, oval, extending onto Finger I; in male, tubercle continuous with nuptial pad; outer palmar tubercle large, distinct, subcircular; subarticular tubercle, large, round, present proximally on each finger, tubercle of Finger I very large; distal subarticular tubercles present on Fingers III and IV; each finger with at least one small supernumerary palmar tubercle proximally; larger supernumerary tubercle between inner and outer palmar tubercles; nuptial spines small, keratinous, distinctly conical, present on dorsal and ventral surface of thumb. Hind limb length (foot plus tibia) 88.4–93.3% of SVL ($\bar{x}$ = 90.8 ± 3.5; n =2); length of toes in decreasing order: IV > III > V > II > I; webbing formula (range followed by mode; n = 3): I 1½—(2⁺–2⅓; 2⁺) II (1⁺– 1⅓; 1⅓)—3 III (2–2⁺; 2)—(3⁺–3½; 3⁺) IV 3⁺—1 V; webbing diminishing distally to form lateral fringes along edges of toes; tips of toes spherical, roughly equal in size to fingertips; inner metatarsal tubercle large, elliptical, raised; outer metatarsal tubercle ovoid, large, two-thirds size of inner; subarticular tubercles well developed, round, distributed on toes as follows: I(1), II(1), III(2), IV(3), V(2); supernumerary plantar tubercles proximally on Toes II–V in some individuals, small, indistinct; tarsal fold weak, extending approximately two-thirds length of tarsus, confluent distally with fringe along inner margin of Toe I.

Skin of dorsum and venter smooth; skin ventral to cloaca pustular, forelimbs slightly pustular, skin on forelimbs and throat slightly creased; cloacal opening round, unornamented, and directed posteriorly at upper level of thigh.

Color in preservative: Dorsum, dorsal surfaces of limbs, ventral surface of forearm and tarsus, palms, and soles dull gray or brown; dorsum with fine speckling of small dark flecks; venter, throat and underside of limbs dull yellow with small, dull, gray or brown spots (these spots obscure most of the yellow ventral color in one individual, KU 218467); tips of fingers and toes yellowish cream; tubercles on hands and feet pale gray. Color in life unknown.

Measurements of holotype (in mm; measurements of adult female paratype in parentheses): SVL 68.9 (77.3), TIBL 30.1 (33.7), FOOT 34.2 (34.6), HLEN 22.8 (22.2), HWID 27.0 (30.3), IOD 4.5 (4.8), IND 4.7 (4.3), ENOS 4.4 (4.8), EYE 6.1 (6.3), HNDL 16.8 (17.3), THBL 11.0 (11.7), RDL 19.3 (20.0).

Distribution.—Known only from the type locality in the Cordillera Occidental (Fig. 1).

Ecology.—According to field notes of F. G. Thompson, the type series was collected in a densely vegetated roadside marsh in an "open pasture."

The marsh was fed by a brook draining into the Rio Moche, and was in the Very Humid Subalpine Páramo life zone. The frogs were active and abundant in pools and running water by day (13:30 h) and were found simultaneously with *Telmatobius degener*.

Etymology.—The specific name (a noun in the genitive case) is a patronym for Fred G. Thompson of the University of Florida, who collected the type series of this species and of *T. degener*, and made several other important collections of *Telmatobius* in northern Peru.

Telmatobius truebae new species
Figure 9

Holotype.—KU 181528, an adult male from Pomacochas (= Florida; 5°49' S, 77°55' W), 2180 m, Departamento Amazonas, Peru, one of a series collected on 4 March 1979 by Thomas J. Berger, David C. Cannatella, and William E. Duellman.

Paratypes.—KU 181492–527, 181529–36 (181536 is a dry skeleton) collected with holotype; 181855 (series of tadpoles) collected by W. E. Duellman, same data as holotype; 212465–72, 212465–76, 212477–80 (cleared-and-stained skeletons) from the type locality collected 29–30 January 1989 and 14 February 1989 by Fernando M. Cuadros, William E. Duellman, and John J. Wiens.

Referred Specimens.—See Appendix I.

Diagnosis.—(1) Premaxillary teeth present; (2) tympanum absent; (3) nuptial spines large, conical, on dorsal surface of thumb; nuptial pad separate from inner palmar tubercle; (4) dorsum (in life) dull brown, gray or olive-green with or without darker spots; (5) venter gray, usually (90%) with yellow to lavender mottling on underside of limbs; (6) skin of dorsum usually (82%) with warts; (7) snout-vent length of males to 68.9 mm, females to 82.0 mm.

The large nuptial spines, large size, and dull gray-brown dorsal color easily distinguish *T. truebae* from all other species in the region except for *T. colanensis* and *T. necopinus*. *Telmatobius truebae* can be distinguished from *T. colanensis* in having: (1) nuptial spines larger, (2) eye less protuberant on top of head, (3) snout usually longer, (3) dorsum usually (82%) tuberculate, (4) toes less extensively webbed, (5) inner palmar tubercle usually smaller, less distinct (in males), and (6) inner metatarsal tubercle smaller, lower, more elliptical. From *T. necopinus*, *T. truebae* differs in the following characters: (1) dorsum usually (82%) tuberculate (smooth in *T. necopinus*), (2) dorsum lacking yellowish flecks (variable in *T. necopinus*), (3) underside of limbs usually (90%) with bright mottling, (4) nuptial spines always large (smaller in one of two males of *T. necopinus*), (5) outer metatarsal tubercle usually larger (greater than one-fourth size inner meta-

tarsal tubercle), (6) nasal not slender and not distinctly curved anteriorly (at midlength), (7) zygomatic ramus of squamosal shorter, (8) median process of sphenethmoid absent, not extending between nasals, (9) median ramus of pterygoid not bent posteriorly or expanded at articulation with prootic, (10) tympanic annulus not reduced to paired vestiges, (11) posterior margin of coronoid process of angulosplenial convex, (12) process on hyale medially oriented or absent, (13) Presacral VIII and sacral vertebrae not fused, (14) clavicle extending to dorsal tip of pars acromialis of scapula. *Telmatobius truebae* also is distinct electrophoretically from *T. necopinus;* they share no alleles at five loci (Ada, Gpi, Me-1, Pep-B-2, Sdh) and parsimony analysis of the allozyme data shows they are not sister taxa.

Description.—Head as wide or narrower than body; head wider than long (HLEN 72.5–85.8% of HWID; $\bar{x} = 79.3 \pm 3.3$, $n = 36$); head length 26.6–31.5% of SVL ($\bar{x} = 29.0 \pm 1.1$, $n = 36$); head width 34.4–40.0% of SVL ($x = 36.6 \pm 1.3$, $n = 36$); nostril on anterior terminus of snout, not protuberant; canthus rostralis indistinct and concave in dorsal profile; loreal region concave; snout moderately short and bluntly rounded in dorsal view and lateral profile; eye anterolaterally oriented, not or only slightly protruding on top of head; eye diameter 25.9–38.0% of head length ($\bar{x} = 29.0 \pm 2.3$, $n = 36$); tympanum absent; tympanic annulus present; supratympanic fold usually well developed, often strongly warty; vertical fold posterior to jaw thick. Maxillary and premaxillary teeth fanglike, embedded in labial mucosa; dentigerous processes of vomers closer to small, subcircular choanae than to each other; processes medial or slightly posterior to level of choanae; oriented perpendicular to longitudinal axis of head (or with slight posteromedial inclination); each process bearing 0–5 ($\bar{x} = 2.6$, $n = 108$) fanglike teeth; vomerine teeth absent on one process in eight individuals, two individuals lacking vomerine teeth entirely (all 10 individuals lacking teeth are from type locality); teeth embedded in buccal lining for most of their lengths. Tongue large, subcircular, attached anteriorly for three-fourths of its length; free and unnotched (or only shallowly notched) posteriorly. Vocal slits absent.

Forelimbs robust in males, relatively slender in females; dermal wrist fold usually present; relative lengths of fingers: III > I ≥ IV > II; palmar webbing absent; lateral fringes absent or very poorly developed; fringe on outer margin of thumb in males well developed; tips of fingers spherical; inner palmar tubercle oval, approximately equal in size to outer; outer margin distinct; inner margin indistinct, continuous with skin of palm; inner palmar tubercle separate from nuptial pad in males; outer palmar tubercle large, flat, circular to ovoid; inner distal margin concave with small supernumerary tubercle either adjacent to margin or fused to it in all specimens from Pomacochas; subarticular tubercles small, round, present proximally on Fingers II–IV; subarticular tubercle on Finger I approxi-

mately twice size of tubercles on other fingers; distal subarticular tubercles small, round, present on Fingers III and IV; at least one supernumerary tubercle present at base of each finger; supernumerary tubercle along outer margin of inner palmar tubercle large; males with large, conical nuptial spines on raised pad on dorsomedial surface of thumb. Hind limb length (foot plus tibia) 80.1–99.9% of SVL ($\bar{x}$ = 90.6 ± 5.0, n = 36); relative lengths of toes: IV > V ≥ III > II > I; webbing formula (range followed by mode; n = 42): I (1½–2⁻; 1⅔)—(2⁺–2⅔; 2½) II (1–1½; 1⅓)—(2⅔–3⁺; 3) III (1⅔–2⁺; 2)—(3⁺–3½; 3⅓) IV (3⁺–3½; 3⅓)—(1⁺–2; 1½) V; webbing diminishing distally to form lateral fringes along edges of toes; tips of toes spherical, roughly equal in size to fingertips; inner metatarsal tubercle small, oval, raised slightly; outer metatarsal round to oval, one-fourth to two-thirds size of inner (usually one-third); subarticular tubercles round, distinct, distributed on toes as follows: I(1), II(1), III(2), IV(3), V(2); plantar supernumerary tubercles usually absent; tubercles present in some individuals between metatarsal tubercles and at bases of toes; tarsal fold extending approximately one-half length of tarsus, confluent distally with fringe along inner margin of Toe I.

Dorsum usually (82%) with warts; skin of venter, flanks, and limbs smooth; skin ventral to cloaca pustular; forelimbs pustular in some males; cloacal opening round and unornamented at mid-upper level of thigh; transverse fold dorsal to cloaca in some individuals.

Color in preservative: Dorsum gray or brown (with darker spots in some individuals) with similar color on limbs, palms, and soles; venter lighter brown or gray with fine gray and white speckling in some individuals; ventral surfaces of limbs usually (90%) with irregular yellow-white blotches; tips of fingers and toes yellowish white; palmar and plantar tubercles pale gray.

Color in life: (KU 181492–536 from Pomacochas, W. E. Duellman field notes) Dorsum dull olive-green to dark gray with fainter dark spots by day; at night, olive-green to tan with dark olive-green, brown, or black spots; venter and posterior surfaces of thighs dark gray; throat with faint lavender or olive suffusion in some; ventral surfaces of thighs (some) and/or shanks (few) with pale pinkish-orange marks; iris dull bronze with black reticulations. Dorsum dull olive-green to brown with or without darker spots; belly gray; ventral surfaces of limbs mottled dull orange-yellow and black; iris gold with black flecks (from W. E. Duellman field notes for KU 212458–61 from Abra Barro Negro).

Measurements of holotype (in mm): SVL 68.1, TIBL 30.0, FOOT 30.6, HLEN 20.0, HWID 25.6, IOD 4.8, IND 4.5, ENOS 5.1, EYE 5.7, HNDL 17.6, THBL 12.6, RDL 20.2.

Larvae.—The following description is based on an individual (one of the series KU 181855; Fig. 16C) at Stage 35 from the type locality with the

following measurements (in mm): total length 75.2, body length 29.5, basal tail muscle height 8.6, basal tail muscle width 6.6, maximum dorsal fin height 5.2 located 27.5 from body terminus, maximum ventral fin height 5.0 located 28.6 from body terminus, body height 13.6, body width 17.4, eye diameter 2.4, pupil diameter 0.8, interorbital distance 3.9, narial diameter 0.6, internarial distance 4.9, snout-naris 5.2, naris-eye 3.2, transverse oral disc diameter 6.6.

Body ovoid in dorsal and lateral view; snout bluntly rounded; naris small, round anterolaterally oriented; eyes small, dorsolaterally oriented; spiracular tube lateral, relatively ventral in position, short; vent short, median, unpigmented. Dorsal and ventral fins slightly narrower than depth of caudal musculature at midlength; caudal fins not extending onto body; tail gradually tapering to blunt terminus; caudal musculature very robust, extending onto body dorsally. Mouth large, anteroventral; oral disc ovoid; marginal papillae arranged in double row posteriorly, single row laterally and anteriorly; some papillae darkly pigmented; anterior gap in marginal papillae wide; oral disc with transangular margin; few, scattered intramarginal lateral papillae in angular area; intramarginal mental papillae absent; jaw sheaths keratinized, gently arced, with finely serrated margins; dorsal sheath wider than ventral; labial tooth-row formula 2/3; tooth rows adjacent to jaw sheaths widely interrupted medially.

Color in preservative: Dorsum of body brown; venter mostly unpigmented; intestine visible through skin; caudal musculature with pigment restricted to scattered brown blotches; dorsal fin with few blotches posteriorly, ventral fin with many small blotches throughout its length.

Color in life: (W. E. Duellman field notes for KU 181855) Body and caudal musculature mottled olive-brown with greenish-olive and olive-black flecks; venter gray; venter lavender anteriorly; fins translucent tan with dark brown flecks; iris pale yellowish bronze.

Variation: Individuals from near Chachapoyas (KU 212504) appear to have longer tails but are otherwise similar to individuals in the series KU 181855. Two large tadpoles (KU 181856, Stage 38, total length 82.2 and 83.2) from the Abra Barro Negro may be assignable to this species (but *T. atahualpai* also occurs at this locality). These specimens differ from KU 181856 and KU 212504 in having more heavily pigmented caudal musculature and a dark peritoneum covering the intestine.

Distribution.—*Telmatobius truebae* is known from several localities in the Cordillera Oriental (Fig. 1) at elevations from 2150–3470 m (Fig. 2).

Ecology.—Specimens were under rocks in or along streams by day and in drainage ditches by night (in Pomacochas). This species occurs in Humid Lower Montane Forest, Very Humid Montane Forest, and Very Humid Subalpine Páramo. Near the Abra Barro Negro, *Telmatobius truebae* was collected with *Gastrotheca monticola*, *Eleutherodactylus* sp.

(*unistrigatus* group), *Phyllonastes lynchi*, *Phrynopus* sp., and *T. atahualpai*. In Pomacochas, *T. truebae* was collected with *Colostethus* sp., *Gastrotheca monticola*, and *Scinax oreites*. The stomachs of three individuals (KU 212464, 212477, and 212480) contained several beetles (Coleoptera: Carabidae, Curculionidae, Staphylinidae), a leafhopper (Homoptera, Cicadellidae), various flies (Diptera: Nematocera and Syrphidae), an ant (Hymenoptera, Formicidae), lepidopterans (adult parts and larvae), two roaches (Blatoidea), a spider, and several millipedes (Diploda: Polydesmidae). Tadpoles were found in pools in streams in late January and early March.

Etymology.—The specific name (a noun in the genitive case) is a patronym for Linda Trueb, in recognition for her many contributions to anuran morphology and systematics, especially of *Telmatobius*.

Finally, I thank Les Marcus for providing the SAS code for the shearing technique, Adrian Nieto Montes de Oca for correcting my translation of the Spanish summary, Richard Leschen for identifying invertebrates removed from stomachs, Luis A. Coloma and John E. Simmons for assistance with the photographic prints, Antonio W. Salas and Linda Trueb for discussions of *Telmatobius* systematics, and David C. Cannatella, Paul Chippindale, William E. Duellman, David A. Kizirian, Linda Trueb, and an anonymous reviewer for helpful criticism of the manuscript.

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APPENDIX I
SPECIMENS EXAMINED

All localities are in Peru. Kilometer distances are by road. Abbreviations are as follows: (AA) alizarin-alcian–stained skeletal specimen, (D) dry skeletal specimen, (E) specimen examined electrophoretically, (T) series of larvae.

Telmatobius atahualpai.—Amazonas: 41 km SW Leimebamba, 3600 m, UF 39715; 28.3 km SSW Leimebamba, 3450 m, KU 182084; N slope Abra Barro Negro, 28 km SSW Leimebamba, 3470 m, KU 212485.

Telmatobius brevipes.—Cajamarca: 23 km SW Celendín, 3050 m, KU 181425–34, 181435 (AA), 181836–37, 181842–44 (T); Sendamal, 30 km S Celendín on Cajamarca road, ca 2530 m, KU 196611, LSUMZ 32261–62; 24 km N Cajamarca, UF 39709–14; S slope Abra Quilsh, 21 km NNW Cajamarca, 3400 m, KU 212412–13 (E); S slope Abra Quilsh, 26 km NNW Cajamarca, 3500 m, KU 212414; 4 km E Baños del Inca, 2900 m, KU 212415–19, 212503 (T); 7 km S Cajamarca, 3010 m, KU 212420–22; 8 km S Cajamarca, 3050 m, KU 212423–24 (E), 212425–27; 3 km SW Encañada, 2980 m, KU 212428–31; Abra Comulica, 20 km NE Encañada, 3420 m, KU 181486–87; S slope Abra Comulica, 20 km NE Encañada, 3420–3520 m, KU 181857 (T), 212432–34; 2 km E Celendín, 2650 m, KU 212441–43; 9 km S Celendín, 2750 m, KU 212444 (E), 212445, 212446 (AA), 212525 (T); S slope Abra El Gavilan, 18.5 km N San Juan, 2920–3100 m, KU 181489 (D), 181491; 12 km SSE Namora, 2000 m, KU 212528 (T); 10 km SSE Cajabamba, 2900 m, KU 212439–40. La Libertad: Huamachuco, 3350 m, KU 131684–89, 131690 (AA), 131691–94, MHNSM 3739–49; 21 km SW Huamachuco, 3500 m, UF 39757–60, 39762; Laguna Sacsacocha, 12 km E Huamachuco, 3050 m, KU 131695; 19 km SSE Cajabamba, 2690 m, KU 212435, 212436–37 (E), 212438, 212447 (AA, E).

Telmatobius colanensis.—Amazonas: SE La Peca, (ca. 5°34'S, 78°19'W), Cordillera Colán, 2410 m, LSUMZ 37102.

Telmatobius degener.—La Libertad: 13 km ESE Yamobamba, 18 km SE Agallpampa on road from Otuzco to Huamachuco, 3290 m, KU 218463–64, 218465 (D), 218466 (AA), UF 39736, 39738–41, 39743–45, 39748–49, 39752–53, 39755.

Telmatobius ignavus.—Piura: 29 km E Canchaque, 2530 m, UF 34089;

29 km E Canchaque, 1840 m, UF 52148; 16 km E Canchaque, 2042 m, UF 52147; El Tambo, 31.5 km E Canchaque, 2770 m, KU 181440 (D), 181441 (AA), 181442–43, 181845 (T), 219821; 12.7 km E El Tambo, 2820 m, KU 219822, 219823 (T), MHNSM 15466–67, 15468 (T); 9.5 km SW Huancabamba, 2320 m, KU 181846 (T); 25.5 km SW Huancabamba, 3010 m, KU 181438–39; 31 km SW Huancabamba, 3080 m,KU 181847 (T); Huancabamba, 2000 m, MCZ 4093.

Telmatobius latirostris.—Cajamarca: Cutervo, 2620 m, KU 212448, 212449–50 (E), 212451 (AA, E), MHNSM 3729–338.

Telmatobius necopinus.—Amazonas: E slope Abra Pardo de Miguel, 39 km ENE Pomacochas (Florida) on road to Moyobamba, 2050 m, KU 212481 (E), 212482, 212483 (E), 212484 (AA, E).

Telmatobius thompsoni.—La Libertad: 13 km ESE Yamobamba, 18 km SE Agallpampa on road from Otuzco to Huamachuco, 3290 m, KU 218467, 218468 (D), 218469 (AA), UF 39734, 39747, 39754, 39756.

Telmatobius truebae.—Amazonas: E slope Abra Chanchillo, 42 km ENE Balsas, 2870 m, KU 212454; 44 km ENE Balsas, 2940 m, KU 212464 (AA); 11 km SE Chachapoyas, 2840 m, KU 212463 (E), 212504 (T); N slope Abra Barro Negro, 28 km SSW Leimebamba, 3470 m, KU 212455 (E), 212456 (E), 212457–61; 28.3 km SSW Leimebamba, 3450 m, KU 181485; 27 km SSW Leimebamba, 3440 m, KU 212462; Pomacochas (= Florida), 2150 m, KU 181492–535, 181436 (D), 181855 (T), 212465–72, 212474–76 (E), 212477–80 (AA), MHNSM 12363–70.

APPENDIX II
OTHER TELMATOBIINES EXAMINED

All specimens are in The University of Kansas Museum of Natural History (KU). Skeletal preparations stained for alizarin-red only (bone only, cartilage not stained) are noted by AR; dry skeletal preparations are noted by DS. For alcoholic specimens, only the males examined are listed.

Osteological.—*Alsodes gargola* 203317 (AR). *Alsodes montanus* 203350 (AR). *Alsodes vanzolinii* 162247 (DS). *Atelognathus patagonicus* 203332 (AR); 160467–68 (DS). *Atelognathus reverbii* 203342 (AR). *Batrachophrynus macrostomus* KU 98127–28 (DS). *Batrachyla leptopus* 161448 (AR). *Batrachyla taeniata* 161489, 161496 (AR). *Eupsophus roseus* 162137–38 (AR); 162204, 187646 (DS). *Eupsophus vertebralis* 162238 (DS). *Hylorina sylvatica* 161407–08 (DS). *Insuetophrynus acarpicus* 161429–30, 203352 (AR). *Lynchophrys brachydactylus* 217152 (AR). *Somuncuria somuncurensis* 203348–49 (AR). *Telmatobufo venustus* 159811, 161439 (DS). *Thoropa miliaris* 92856, 186760 (DS).

Telmatobius arequipensis 164078 (DS). *Telmatobius carrillae* 214825 (DS). *Telmatobius ceiorum* 160848 (DS). *Telmatobius cirrhacelis* 165989

(DS). *Telmatobius culeus* 135864 (DS). *Telmatobius hintoni* 160190–91 (DS). *Telmatobius jelskii* 164081, 181835 (DS). *Telmatobius marmoratus* 135903–04, 164079–80 (DS). *Telmatobius niger* 131796 (DS). *Telmatobius oxycephalus* 128880 (DS). *Telmatobius peruvianus* 162113–14 (DS). *Telmatobius schreiteri* 160885–86 (DS). *Telmatobius simonsi* 160139 (DS). *Telmatobius vellardi* 120292 (DS).

External.—*Alsodes monticola* 160568, 160573. *Alsodes vanzolinii* 162207, 162222. *Atelognathus patagonicus* 160427–28, 160430. *Atelognathus praebasalticus* 180992. *Atelognathus salai* 192117. *Atelognathus reverbii* 180997. *Batrachyla antarandica* 161497–98, 161501. *Batrachyla leptopus* 161440, 161446. *Caudiverbera caudiverbera* 161411–12. *Eupsophus roseus* 160562, 160564–65. *Eupsophus vertebralis* 162241. *Hylorina sylvatica* 161399, 161405, 161410. *Insuetophrynus acarpicus* 161413. *Lynchophrys brachydactylus* 217151, 217153. *Telmatobufo venustus* 161438. *Thoropa lutzi* 92846–48. *Thoropa miliaris* 74203, 92854. *Thoropa petropolitana* 92858.

Telmatobius arequipensis 194900, 194903. *Telmatobius atacamensis* 179739–40. *Telmatobius carrillae* 214823. *Telmatobius ceiorum* 160846–47. *Telmatobius culeus* 135869, 183138, 183143. *Telmatobius halli* 159840. *Telmatobius hauthali* 182848–49. *Telmatobius hintoni* 160160. *Telmatobius jelskii* 181460, 181463. *Telmatobius laticeps* 182837. *Telmatobius marmoratus* 135893, 135895, 135898. *Telmatobius niger* 131782, 131785, 165976. *Telmatobius oxycephalus* 128875–76. *Telmatobius peruvianus* 162058, 162060. *Telmatobius schreiteri* 160856, 160861, 160883. *Telmatobius stephani* 206702.

APPENDIX III
APOMORPHY LISTS

Character state optimizations and FREQPARS branch lengths are given for each stem of the unrooted tree preferred by PAUP and FREQPARS analyses (Fig. 17A). Allelic changes are superscripted (but left-to-right sequence does not necessarily indicate primitive-to-derived transition); ambiguously placed transformations are followed by the optimization routine that places them at that stem.

Stem 1.—PAUP: Pgm^{ab-aa}, Sdh^{bb-bc}. FREQPARS: 3.00.

Stem 2.—PAUP: Adh^{ee-be} (DELTRAN), $Me\text{-}2^{bb-ab}$. FREQPARS: 2.50.

Stem 3.—PAUP: Adh^{dd-ee}, $G3pdh^{cc-bb}$, $Hbdh^{bb-cc}$, $Icdh\text{-}2^{aa-bb}$, $Ldh\text{-}2^{aa-bb}$, $Me\text{-}1^{bb-aa}$ (ACCTRAN), $Me\text{-}2^{cc-bb}$, Mpi^{cc-bb}. FREQPARS: 16.00.

Stem 4.—PAUP: $Me\text{-}1^{aa-bb}$ (DELTRAN), Pgm^{ab-bb}, Sdh^{bb-aa}. FREQPARS: 3.500.

Stem 5.—PAUP: $G3pdh^{cc-ac}$ (ACCTRAN), Gpi^{aa-bb}. FREQPARS: 2.66.

Stem 6.—PAUP: Mpi^{cc-cd}. FREQPARS: 0.800.

Telmatobius brevipes-1.—PAUP: Adh^{be-ee} (ACCTRAN), Pep-B-1^{ab-aa}, Sod^{aa-ab}. FREQPARS: 0.50.

Telmatobius brevipes-2.—PAUP: Adh^{ee-ce}, Hbdh^{cc-ac}, Mpi^{bb-ab}, Pep-B-2^{aa-ad}, Sod^{aa-abc}. FREQPARS: 2.00.

Telmatobius brevipes-3.—PAUP: Adh^{be-ee} (DELTRAN), Ldh-1^{cc-ee}, Pep-B-1^{aa-dd}, Sdh^{cb-cc}. FREQPARS: 6.00.

Telmatobius brevipes-4.—PAUP: Adh^{be-ab} (ACCTRAN), Adh^{ee-ab} (DELTRAN), Ldh-1^{cc-ac}. FREQPARS: 2.50.

Telmatobius latirostris.—PAUP: Hbdh^{bb-dd}, Ldh-2^{aa-cc}, Pep-B-1^{aa-cc}, Pep-B-2^{aa-bb}. FREQPARS: 8.00.

Telmatobius necopinus.—PAUP: Ada^{bb-aa}, Ldh-1^{cc-cd}, Ldh-2^{aa-ad}, Mdh-2^{bb-ab}, Me-1^{bb-cc}, Pep-B-2^{aa-cc}. FREQPARS: 5.16.

Telmatobius truebae-1.—PAUP: G3pdh^{cc-ac} (DELTRAN), Tpi^{aa-ab}. FREQPARS: 2.00.

Telmatobius truebae-2.—PAUP: G3pdh^{ac-cc} (ACCTRAN), Me-2^{cc-cd}. FREQPARS: 1.20.

Telmatobius truebae-3.—PAUP: Aat^{aa-ab}, G3pdh^{cc-ac} (DELTRAN), Ldh-1^{cc-cb}, Mdh-2^{bb-ab}, Pgm^{bb-ab}. FREQPARS: 2.26.